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CONTENTS

Verticillium Hadromycosis

B. A. RUDOLPH

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B. A. RUDOLPH

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VERTICILLIUM HADROMYCOSIS[1]

B. A. RUDOLPH[2]

REVIEW OF THE CONTENTS

Verticillium hadromycosis is a plant disease specifically caused by the fungus *Verticillium albo-atrum* R. and B. and its related forms. It is widespread in the United States and abroad. At present it is occasioning considerable economic loss in the coastal counties of California.

The parasite is peculiar in that it does not confine its attacks to one host, or a few closely related hosts, as is so frequently the case with parasitic fungi, but attacks a large number of widely unrelated plants, many of which are of economic importance.

The disease syndrome is essentially as follows: The lower leaves of affected plants turn yellow in early summer and die as the parasite, which initiates its attack through the root system, passes slowly up the trunk or stem. The internodes are shortened and the plant is stunted. Internally the affected wood shows a characteristic brown discoloration. With the microscope the mycelium of the fungus may be seen in the lumina of the vessels of the discolored wood.

In annuals such as the tomato, potato, and other susceptible truck-crop plants an attack of the disease is generally fatal. Perennials such as economic fruit and forest trees, particularly when young, may be killed, or they may recover, depending upon the severity of the attack.

In California, the disease is referred to popularly as 'black heart' in stone fruits, 'blue stem' in bush fruits and 'wilt' in truck-crop plants. The syndrome in affected plants of these three distinct groups may vary somewhat, but the cultural similarity of the organisms isolated from them has led to cross-inoculation experiments by the author to determine whether the seemingly three distinct diseases are not of common origin, a fact previously not suspected in California.

Myrobalan seedlings and raspberry and tomato plants were selected as representative of the three groups, and cross-inoculations

[1] The term 'hadromycosis' was first suggested by Pethybridge (149) for this peculiar form of disease in which the parasite is confined almost exclusively to the xylem (hadrome). Other terms suggested are 'tracheo-mycosis' (Quanjer, 158; van der Lek, 188; van der Meer, 191) and 'vascular mycosis' (Appel, 7; and others). These terms are not beyond criticism since the xylem alone is involved, and as Pethybridge (149) has pointed out, they are awkward to use.

[2] Assistant Plant Pathologist in the Experiment Station.

were made with pure cultures of the parasite isolated from affected plants in these groups. The results of the experiments conducted over a period of several years, which prove that the disease is intercommunicable within the groups, are given.

In addition, proof is given that the strain of the organism which attacks the tomato and kills it, also readily attacks the apricot. This fact is of considerable economic importance; in California young apricot orchards are commonly interplanted with tomatoes. The investigations show that the tomato, a very susceptible plant, readily contracts the disease, propagates the fungus and aids in its dissemination in the soil, where it eventually reaches and attacks the roots of the apricot trees. Experiments with seventeen of the better known varieties of tomatoes, conducted over a period of several years, have shown that resistance to the disease in the tomato is very low.

The investigations show that the disease also attacks some of the commonest weeds, such as the mallow plant, rough pigweed, bur clover, dandelion, and groundsel, all of which abound in California. Such weeds are a menace when left to grow uncontrolled in orchards and truck and berry patches, as they may contract the disease and thereby help to establish the fungus in the soil.

Since the disease was first described in Germany in 1879 by Reinke and Berthold, who observed it in the potato, reports of the susceptibility of other plants have appeared with unusual frequency. The host tables which have appeared in the literature, however, are only fragmentary and never sufficiently inclusive. Similarly, neither a sufficiently comprehensive digest of the vast literature which has accumulated on the subject nor a satisfactory bibliography has appeared. In the present paper a digest of the literature from 1879 up to and including 1928 has been made. This paper was written in 1929. Occasional references to papers which appeared during the early part of that year have been made. The individual history of the disease in each known host is given, as well as a bibliography pertaining to the disease in each host. It is hoped the present paper will be of help to professional plant pathologists and obviate much of the tedious search through the literature which is inevitable now when complete information of a bibliographical nature is desired.

The bibliography is acknowledged to be incomplete. In general, newspaper articles or unsigned popular accounts of the disease which have appeared in obscure places of publication, as well as certain text-book descriptions have been omitted purposely, especially when these articles have not been supported by investigational data or have

not contributed to knowledge already established by other workers. It may be that certain technical papers of importance have been overlooked, particularly those of German origin. This has not been intentional.

The search through the literature has revealed that the disease has been reported definitely in over one hundred and twenty species included in thirty-five widely unrelated families and eighteen orders.

Since Reinke and Berthold first described the disease in potato and proved it to be due to a fungus which they named *Verticillium alboatrum,* a number of new species of *Verticillium,* said to produce the same disease in other plants, have been described. In most instances the claim of these organisms to specific rank is exceedingly doubtful. The most conspicuous of these is *Verticillium dahliae* Klebahn. Evidence is advanced to show that this fungus is not entitled to specific rank. The taxonomic relationship of the other putative species also is discussed.

INTRODUCTION

The seriousness of *Verticillium* hadromycosis in economic, ornamental, and weed plants in California is becoming more and more appreciated every year. The disease is referred to popularly as 'wilt' in truck crops, 'blue stem' in bush fruits and 'black heart' in stone fruits, according to the concomitant symptoms produced.

In Germany, the disease as it affects potatoes, has been referred to in the past as *Kräuselkrankheit* and *Blattrollkrankheit,* which names are applied now to two distinct diseases of nonparasitic or, at least, obscure origin, in association with which *Verticillium* hadromycosis may occur at times. The utmost confusion prevailed for years in European literature, particularly that of Germany, regarding the nature and etiology of the two diseases referred to, as the following outline is designed to show.

According to Appel and Schlumberger (5, 8),[3] Pethybridge (149), and others, *Kräuselkrankheit* (curl; leaf-curl; curly dwarf, etc.), was observed in Europe as early as the last half of the eighteenth century, both in England and on the continent. Since that time, the nature and etiology of the disease have been the subject of heated discussion between a great many writers. As early as 1804, Forsyth[4] had pub-

[3] Reference is made by number in parentheses to "Literature Cited," page 335. The publications in this list deal directly with *Verticillium* hadromycosis. Literature cited in footnotes ordinarily is not concerned with *Verticillium* hadromycosis.

[4] Forsyth, Robert. The principles and practice of agriculture. Encyclopedia Britannica. 4th ed. 1:174–193. 1804.

lished a digest of the twenty or thirty distinct theories which had been advanced up to that time. Many of them are fanciful in the extreme.

In 1906 Appel (5, 6), pointed out that the term *Kräuselkrankheit* as then used, embraced several distinct diseases to which he referred (5) as *Kräuselkrankheit, Bakterienringkrankheit,* and a third which he named *Blattrollkrankheit. Blattrollkrankheit* he regarded of fungus origin, saying (5):

> With this name I refer to a disease which of later years has been overlooked entirely but which appears in the literature under the collective conception '*Kräuselkrankheit.*' It was very clearly described by Schacht[5] who noticed it in isolated cases in the *Phytophthora* year 1854. Also, the *Kräuselkrankheit* described by Reinke and Berthold (164) belongs to this type.

While Appel regarded Reinke and Berthold's disease (due to *Verticillium albo-atrum*) as of the same type as *Blattrollkrankheit,* he regarded true *Blattrollkrankheit* as due to *Fusarium.*

Appel's contention that the term *Kräuselkrankheit* embraced several distinct diseases was accepted readily by writers at the time, but differences of opinion arose almost at once as to the etiology of the disease which he had named *Blattrollkrankheit.* Some championed Appel's *Fusarium* hypothesis, but others considered the disease to be of non-parasitic origin or due to parasites other than *Fusarium.* A new controversy arose over the nature and etiology of this disease which became as heated as the earlier one on *Kräuselkrankheit* had been.

According to Appel and Schlumberger (8), as early as 1909 Spieckermann (179)[6] had recognized that the term *Blattrollkrankheit* embraced at least two distinct diseases, one of fungus origin (*Verticillium*) and the other non-parasitic. In 1910, Spieckermann (180) reiterated this opinion, but his work seems not to have been appreciated at the time. It was not until Orton's paper (135) appeared in 1913 that any headway was made in unraveling the tangle. Orton regarded *Kräuselkrankheit* and *Blattrollkrankheit* as two distinct diseases of unknown or obscure origin. Those due to *Verticillium* and *Fusarium* he classified as 'wilts.' Orton's classification has been accepted by writers generally. It is clear now in looking over the older literature, particularly that of Germany, that many workers were dealing with hadromycosis due to *Fusarium* or *Verticillium,*

[5] Schacht, Herman. Bericht an das Königliche Landes-oekonomie-kollegium über die Kartoffelpflanze und deren Krankheiten. p. 15. table 6. figs. 11, 12. K. Wiegandt, Berlin. 1856.

[6] This paper is not available in the United States.

alone or in association with *Blattrollkrankheit* or *Kräuselkrankheit*, but failed to recognize the fact. Failing in this, their observations frequently were incorrect or incorrectly interpreted. Papers of this kind have not been included in the bibliography for obvious reasons.[7]

HISTORY OF VERTICILLIUM HADROMYCOSIS

The earliest authentic reference we have to this disease is, by common consent, the work of Reinke and Berthold (164) which appeared in 1879. These workers isolated a fungus from potato plants affected with a disease referred to at the time as *Kräuselkrankheit*. They named this fungus *Verticillium albo-atrum*. Their work was lost sight of for nearly thirty years, and it was only brought to light again when the attention of investigators was forced upon such diseases of *Solanum tuberosum* as *Blattrollkrankheit* and *Kräuselkrankheit*, which were raising havoc in Europe the early part of the present century.

In 1904, Van Hook (194) described a typical case of hadromycosis in ginseng (*Panax quinquefolium* L.), which he attributed to *Acrostalagmus albus* Pr. After the appearance of his paper, wilt diseases due to *Acrostalagmus* were reported both in North America and Europe.

The generic name *Acrostalagmus* is a *nomen nudum* because it is synonymous with the older genus *Verticillium*.

Identification of the Genus Acrostalagmus with Verticillium.—The genus *Verticillium* was created by Nees von Esenbeck[8] in 1816. Corda[9] described the genus *Acrostalagmus* in 1838.

In 1854, Hoffman[10] advanced proof that no real difference exists in the manner in which the spores of these two organisms are pro-

[7] Appel and Schlumberger (8) prepared an excellent though by no means complete digest of the literature prior to 1911 which deals with the *Blattrollkrankheit* controversy. Over one hundred and fifty papers were reviewed, among which at least sixteen distinct hypotheses concerned with the etiology of the disease have been advanced. One hypothesis, namely, that the disease is of fungus origin, involves at least eight distantly related organisms. It is interesting to note, however, that *Verticillium* and *Fusarium* were held responsible by most writers who supported the fungus theory. Appel himself attributed *Blattrollkrankheit* to *Fusarium*. Later he accepted Orton's classification (7).

[8] Nees von Esenbeck, C. G. Das System der Pilze und Schwämme. 329 p. 46 pl. Stahelschen Buchhandlung, Würzburg. 1816.

[9] Corda, A. Icones fungorum 2:15. J. G. Calve, Prague. 1838.

[10] Hoffman, H. Spermatien bei einem Fadenpilze. Bot. Zeit. 12 (15 and 16): 249–254, 265–269. 1854.

duced or in the manner in which they are united in heads, hitherto regarded as the chief distinctions between them. Reinke and Berthold (164) accepted Hoffman's views and referred the organism which they had just isolated from potatoes to the genus *Verticillium*, calling it specifically *V. albo-atrum* (plates 1 and 2).

Carpenter (49) further sums up the situation:

Corda established the genus *Acrostalagmus* to accommodate an organism, *A. cinnabarinus*, which was said to differ from *Verticillium* by forming its spores in heads at the tips of the conidiophores. Hoffman has rightly explained the complicated structure of the sterigma as represented by Corda, and likewise the collection in heads of the singly abscissed conidia. The conidia are held together by virtue of an hygroscopic slime, which takes up water in the presence of a sufficiently moist atmosphere, forming a sphere of water at the tip of each sterigma. In these water droplets the conidia are observed to float freely. With excess moisture the drops rupture and the conidia slip down the conidiophore. However, in the absence of moisture the conidia cling tenaciously to the tips of the sterigma in the form of irregular rounded masses of varying size. If such material is placed under a dry cover slip without being allowed to come in contact with the latter, and examined microscopically while a small water drop is brought into the vicinity of the dry spore head, the spore aggregate will be seen gradually to round up and the conidia to float more or less actively within the spherule.

In the genera *Acrostalagmus* and *Verticillium* we now have the following contradictory and imperfect characterization and limitation of forms. In *Verticillium* the singly abscissed and characteristically singly borne conidia may adhere in the presence of moisture, forming terminal heads—that is, water droplets containing conidia. In *Acrostalagmus* the conidia, characteristically united in heads, soon separate if the humidity of the environment is in excess of the maximum for the moisture drops to retain their form, leaving but one immature conidium on the sterigma tip, as in *Verticillium*.

Furthermore, in the genus *Verticillium*, characterized by singly borne or readily separating conidia, we have the anomalous condition of a section of the genus set aside for those species in which the conidia are held together by slime—that is, section *Gliocephalum*[11] Saccardo (1886). This section of the genus accommodates forms in which the conidia are united in slimy heads—that is, *Acrostalagmus*.

The fact that the work of Reinke and Berthold was so generally overlooked is responsible for the confusion of the genera *Verticillium* and *Acrostalagmus*. These investigators studied *A. cinnabarinus*, on which Corda established his genus *Acrostalagmus*, and concluded that this form genus must be united with the older genus *Verticillium* Nees. They changed the name of Corda's fungus to *Verticillium cinnabarinum*. In view of the above, there seems to be no doubt that the genus *Acrostalagmus* Corda should be united with the genus *Verticillium* Nees.

[11] Saccardo's section *Gliocephalum* of the genus *Verticillium* (Saccardo, P. A. Sylloge fungorum **4**:159. Patavii, Italy. 1886) is given as *Gliocladium* by Engler and Prantl, apparently through error. (Engler, A. and K. Prantl. Natürlichen Pflanzenfamilien **1**(1):418, 432. Leipzig. 1900.)

Klebahn's (113) views are identical with Carpenter's. Among other writers who regard the two genera as synonomous may be mentioned van der Lek (188, 189), Westerdijk[12] (205), Foëx (77) and van der Meer (191).

Accordingly, the several species of *Acrostalagmus* associated with hadromycosis of economic and ornamental plants should be referred to the genus *Verticillium*—probably to *V. albo-atrum,* which they resemble so closely in most instances that it is doubtful whether they are entitled to specific rank. Until a monograph of the genus is written, however, substantiated by cross-inoculation experiments and morphological and physiological studies, it would probably be best to refer them to the genus *Verticillium,* but to continue using the specific names already given them. Thus *Acrostalagmus albus* described on ginseng by Van Hook (194) should be called *Verticillium albus.* This fungus was renamed *A. panax* by Rankin (159), who gave neither reasons for making the change nor a description of the fungus.

Similarly the following species of *Acrostalagmus* associated with hadromycosis should be classified under *Verticillium: A. vilmorinii* Guéguen described in 1906 and said by the author (82) to produce a wilt of the China aster (Reine-marguerite); *A. caulophagus* Law. described in 1912 (117), and said by the author to produce 'blue stem' of the black raspberry (*Rubus occidentalis*); *Acrostalagmus* sp. referred to as the cause of a thrombotic disease of maples by Rankin (160) in 1914.

Later References to Verticillium Hadromycosis in the Literature.—Although proved by Reinke and Berthold (164) in 1879 to be the cause of a hadromycosis in potato plants, the genus *Verticillium* was not mentioned in this connection by its right name in the literature until nearly thirty years later when Aderhold (1) in 1907 described typical cases of the disease in currants and gooseberries, which he attributed to *Verticillium* sp.

In 1909 Störmer (184), Appel (7), Appel and Wollenweber (9), and Spieckermann (179) reported the presence of *Verticillium* in diseased potato plants in Germany. Appel (7) had observed the disease in 1907 and 1908.

In 1910 Pethybridge (142) described a typical case of hadromycosis in a potato plant in Ireland, saying in part: "In one of these cases a fungus has been isolated which proved identical with one obtained thirty years ago by Reinke and Berthold and named by them *Verticillium albo-atrum.*"

[12] Also in a personal letter.

From 1910 to date there has been a steady output of papers totaling over eighty in number, which report *Verticillium* hadromycosis of the potato in various parts of the world. Many give the results of extensive research; some of them are reviewed under "Irish Potato" (p. 265).

In 1913 Klebahn (113) isolated a *Verticillium* from dahlia plants which he considered distinct from *V. albo-atrum* R. and B. He named it *V. dahliae* Kleb. This species has been accepted as authentic by van der Meer (191), Berkeley and Jackson (21), and Dufrenoy (72).

In 1921, Wollenweber (216) in an address before the Society for Applied Botany at Munich, August 10, 1921, mentioned a new species of *Verticillium* which he obtained from diseased lupine plants. He named it *V. angustum.* Its chief distinction from *V. albo-atrum* is said to lie in its smaller conidia. Dr. Wollenweber apparently never published a full description of the fungus, and from the present meager information its claims to specific rank are exceedingly doubtful.

In 1925, Foëx (77) described a species of *Verticillium* isolated from decayed potato tubers which he had obtained from Professor Duboys of the Agricultural School at Rennes, France. Experimentally he demonstrated the ability of the fungus to penetrate the healthy, unbroken epidermis of potato tubers and bring about a complete decay of the inner tissue. The ability of the fungus to produce a hadromycosis of the stems was not established. His experiments were very limited in number and scope, however, and confined to only a very few plants. He was aware that the culture characteristics of his organism do not materially differ from those of *V. albo-atrum* and its many variational forms, and considered its chief claim to specific rank to lie in its ability to produce a decay in potato tubers, a characteristic generally not attributed to *Verticillium albo-atrum* or *V. dahliae.* For this reason with considerable hesitation he named it *V. duboys.* Picado (155) regards *V. duboys* as physiologically distinct from *V. albo-atrum.*

In 1925, Curzi (55) described a typical hadromycosis of pepper plants (*Capsicum annum* L.) which he attributed to a new species of *Verticillium.* He named it *V. tracheiphilum.* From the descriptions of it, it is doubtful whether this organism differs sufficiently from *V. albo-atrum* to justify giving it specific rank. This fungus and *V. duboys* are further discussed under "The Relation of *Verticillium albo-atrum* to Other *Verticillium* Species Known to Produce Hadromycosis in Plants" (p. 252).

In 1926, Berkeley and Jackson (21) described a *Verticillium* which they isolated from red raspberry and which in their opinion differed sufficiently from other species of *Verticillium* already described to justify giving it specific rank. They called it *V. ovatum,* after the oval-shaped spores.

History of the Disease in California.—In California, according to old residents, *Verticillium* hadromycosis was first observed in orchards of stone fruit trees during the first decade of the present century. It had been noticed that interplanting young apricot, plum, peach and almond orchards with tomatoes only too frequently led to an attack of disease in the trees which was then called, and still commonly is called 'black heart.' At the time, the diseased condition of the trees was considered to be either the result of shock following a heavy irrigation of the tomatoes or the result of the souring of the soil by the great quantity of tomatoes left to rot on the ground at the close of the harvest.

In 1915, Phillips (154) presented a paper covering her work on this disease and 'sour sap' at the annual meetings of the Pacific Division of the American Phytopathological Society. She did not associate a fungus parasite with 'black heart.'

In 1916 Czarnecki (57) reported the results of her studies on 'black heart' at the annual meetings of the Pacific Division of the American Phytopathological Society. She presented proof of the fungus origin of the disease and thereby set to rest the numerous vague theories which had been advanced to explain its cause. Only the title of her paper appeared in Phytopathology.

In 1923 Miss Czarnecki's paper (58) appeared and of the causal agent she said: "The cultural work up to the present time indicates that the fungus belongs to the genus *Verticillium* and is apparently a new species, as no previous record of a *Verticillium* of a true parasitic nature inhabiting the sound wood tissue of the apricot, almond, or any other fruit tree has been found."[13]

Miss Czarnecki appreciated the fact that the interplanting of tomatoes in stone-fruit orchards had some direct bearing upon the etiology of the disease: "The disease is most commonly found in three to six-year-old trees which are heavily irrigated during the summer and intercropped with tomatoes."

[13] Miss Czarnecki had completed her paper at the time of her death in 1917. This information will serve to explain her apparent unfamiliarity with the work of others on this problem, particularly that of Haenseler (83), who reported *Verticillium* hadromycosis of the peach in 1921.

She was unaware, however, that *Verticillium* attacks the tomato and never rightly understood the rôle this plant plays in establishing the fungus in the orchards in which it is interplanted.

In 1923, Horne, Essig, and Herms (107) referred to black heart of apricots without giving the cause of the disease. Blue stem of raspberries was attributed to the attack of *Verticillium caulophagus* Law. The identity of the two diseases was not appreciated at the time. No reference to the disease in truck crops was made.

This paper was revised in 1925 without changes in the references to black heart and bluestem. A final revision was made in 1927. Black heart of apricots, bluestem of bush fruits, and wilt of tomato and potato were briefly discussed and attributed to *Verticillium* sp.

In 1926 the writer published a note in Phytopathology (167) giving briefly the results of experiments and observations made during the previous three years and reporting the disease in tomatoes in California for the first time. The interhost relationship of the fungus was established as the result of cross-inoculation experiments made with monosporic cultures of *Verticillium* from stone fruits (apricots and peaches), bush fruits (raspberries) and truck crops (tomatoes).

In June, 1926, a popular account of the experiments (168) was published, and the disease was reported for the first time in certain weed plants. The details of these experiments are given for the first time in a later section of this paper.

The annual report of the University of California Agricultural Experiment Station for 1916 briefly mentions the disease in apricots by common name, and from 1923 to date these reports refer to the disease in various economic crops.

Howard (108), Rosa (166), and Hendrickson (103), have given brief descriptions of the disease in papers written by them.

DESCRIPTION OF VERTICILLIUM HADROMYCOSIS

At this point only those major symptoms which may be expected to occur in any of the widely unrelated plant suscepts are discussed. In a few species the syndromal characteristics vary considerably from the disease picture given here. Such variations are discussed under the individual hosts.

External Symptoms

Leaves.—The first outward symptom of the disease is the defoliation of the affected limbs and stems in early summer. The leaves

become dull looking. The tissue between the veins may blanch slightly, imparting an appearance somewhat reminiscent of a mild chlorosis. This blanching is due to the partial destruction of the chlorophyll. It is not a constant characteristic.

Occasional writers refer to brown spots on the leaves of plants suffering *Verticillium* hadromycosis. It is doubtful whether such spots have any bearing upon the disease. No one seems to have isolated *Verticillium* from them. Reinke and Berthold (164) first reported brown spots on leaves of affected potato plants but expressed doubt as to their significance. Under California conditions, brown spots ordinarily do not occur on affected plants, and if present, may usually be readily associated with other causes. Westerdijk (204) found yellow spots on the outer leaves of beets affected with the disease, and succeeded in isolating the fungus from them. Similarly Bewley (24, 28) reports yellow blotches on the lower leaves of tomatoes. Yellow blotches may or may not occur on the leaves of affected plants in California, but they are the exception rather than the rule. Leaves of affected plants turn yellow and finally brown as they wither and die. Their appearance does not differ materially from that of leaves dying from natural causes.

The lower leaves wilt first and fall as the disease progresses upward from the bottom of the plant to the top. It is not unusual to see raspberry canes in the final stages of the disease devoid of all leaves except for a tuft at the extreme tip. Defoliation from the top of the plant downward never takes place, although this error in observation has been made by Czarnecki (58) and Lawrence (117).

In the case of the raspberry and udo, the blade of the leaf may be cast long before the petiole.

Wilt in its true sense, namely, a flaccid state of the leaves accompanied by a loss of turgor in the shoots, is absent so frequently from the tops of affected plants that considerable discussion has arisen as to the propriety of applying the term 'wilt disease' to this form of malady. The term continues to be used widely, however. In many species, the apricot, for instance, the disease process in the leaves ordinarily seems to be one of simple desiccation. The maple, on the other hand, is said to suffer sudden collapse when seriously attacked, and the leaves show more typical symptoms of wilt. Similarly, the foliage of such annuals as the potato, tomato, and cucumber may display distinct symptoms of wilt during the heat of the day. The leaves frequently hang limp from the stem, and the tender tips of the shoots also droop; this characteristic has led to the use of the term 'sleepy

disease' by English writers. At night the wilted leaves and shoots recover their turgidity to a considerable extent, but the gradual decline of the entire plant continues until death ensues. As the lower leaves wither and die, the terminal growth is slackened, and new leaves formed are markedly smaller in size and present the same dull appearance remarked in all hosts. Occasionally at the base of the stems of tomato and other truck-crop plants from which the old leaves have been shed, new leaves are formed. Invariably they are stunted and very poorly developed.

Trunks, Stems, and Twigs.—With few exceptions, the trunks, stems, and twigs of affected plants show no outward sign of the disease other than a general stunting and curtailment of new growth which is accompanied by a shortening of the internodes. Even after a limb or twig has become totally defoliated, the wood may appear outwardly healthy.

The disease is peculiar in that it may attack any suscept in all parts, or it may be confined sharply to one side or even to only one shoot or limb of the affected plant (fig. 1). Internally the line between the healthy and the diseased wood is sharply drawn, which is in contradistinction to the external symptoms. The maple, which develops lesions on the bark under certain conditions, is an exception to the general rule. Also the stems of certain bush fruits, particularly the gooseberry, tend to become dropsical or edematous. Guéguen (82) states that affected Reine-Marguerites are easily decorticated. Gravatt (81) reports the same of maple. The canes of red and of black raspberries develop characteristic blue-black discolorations which has led to the popular use of such terms as 'bluestem,' 'blue stripe,' etc., in connection with the disease (fig. 2).

If the edema in the canes of bush fruits becomes very severe, the bark may rupture and sap ooze from the lesions so formed (Aderhold, 1; van der Meer, 191, 192; van Poeteren, 196). Under California conditions edema is rarely observed in the stems of affected plants. Occasionally, in the last stages of the disease, the wood of the canes of Ranere raspberries presents a water-soaked appearance.

Gravatt (81) reports a slime flux on the bark of maples suffering the disease.

With the exception of the maple, death seldom results in mature or old forest, ornamental, or economic fruit trees which have been attacked. The older limbs may be considerably altered in appearance within and completely defoliated, but they rarely die. The first-year shoots which develop from older wood frequently are killed,

however. Similarly one-year old nursery stock frequently is killed, and occasionally trees three or four years of age die (fig. 3). Most trees outgrow their susceptibility to attack to a large extent as they grow older.

Ordinarily old wood displays remarkable recuperative powers regardless of the severity of attack. A large limb or an entire tree

Fig. 1. Young Blenheim apricot tree, severely affected on one side with *Verticillium* hadromycosis. Pure cultures of the fungus were obtained from the affected wood of this tree.

completely defoliated one year may not show the slightest outward sign of disease the next. Trees or portions of trees which have suffered a severe attack ordinarily do not grow as rapidly the year following (van der Meer, 191, and author's observations), and if attacked for several consecutive years a young tree is stunted. If only one side or portion of a tree is attacked for several consecutive years the affected side will be dwarfed, giving the tree a lopsided appearance.

Fig. 2. Raspberry canes, Ranere variety, in the last stages of *Verticillium* hadromycosis. The characteristic bluish discoloration which accompanies the disease in raspberries has assumed the form of a stripe in the young cane on the left. The cane on the right is completely girdled by discoloration which reaches almost to the extreme tip. The leaves have been shed except for a terminal tuft.

Annuals such as the potato, tomato, cucumber, and pepper, and bush fruits such as the raspberry, present the same general symptoms in the stems; the internodes are shortened and the plants generally stunted. Death more frequently terminates the course of the disease in these plants, however, than in old woody perennials.

Fig. 3. Young apricot tree, Blenheim variety, killed by *Verticillium* hadromycosis. This tree collapsed rather suddenly. *Verticillium* in pure culture was obtained from the affected wood at many points in the tree. Note the puny tomato plant on the left side of the tree and the stunted pigweed on the right, both of which also were affected with the disease.

During the winter following an attack, the tender twigs of a tree which have been killed by the disease may become covered with dense masses of sclerotia of the parasite. Czarnecki (58) found them on dead apricot twigs and succeeded in producing them on artificially inoculated apricot twigs in the laboratory. I have found them on dead twigs of the prune and also on the tips of dead raspberry canes.

Harris (96, 97) also found them on the bark of raspberry canes. The sclerotia appear as sandy or gritty black particles and are easily rubbed off with the fingers (Guéguen, 82; and author's observations). There are very few references in the literature to the presence of sclerotia on the outer surface of affected twigs, but numerous writers have observed them in the inner tissues, including the vessels, and in the pith of roots and stems.

Under California conditions aerial mycelium or spore fructifications rarely if ever develop on the surface of dying or dead plants in the field, presumably because of the very dry air and absence of rain during the summer season. Reinke and Berthold (164) noted that conidia are produced sparingly or even suppressed when the air is dry. Various writers, however, report the production of aerial mycelium and spores upon the surface of dying stems and twigs in greenhouses and in humid localities; Orton (137) and Bailey (12) report the spore masses on dying potato stems to be dense enough to give the stems a characteristic grey color. Averna-Saccá (10) describes the aerial mycelium on tobacco inflorescences as so dense that the blossoms are stuck together. Other writers who report the production of mycelium and spores on dying leaves and stems of various plants are Bewley (24, 28, 30), Klebahn (113), and van der Lek (190).

Roots.—Externally the roots of most species of plants attacked by the disease show no external lesions or symptoms of any kind. The main roots and rootlets appear normal in size and development. Decay is absent.

The fibrous roots of annuals attacked by the disease generally dry up in the ground as the plant dies.

On tender tap-rooted plants, such as the tomato, the tap root or portion of the stem below ground, as well as the large fibrous roots, may show conspicuous, large, black, irregular cankers (fig. 4). Reinke and Berthold (164) first described lesions on the underground portions of potato stems, but no other investigator seems to have reported them with the exception of Bewley (24, 30) and Klebahn (113). Reporting his studies on tomatoes, Bewley (24, 30) observed: "The fungus destroys the cortex at the point of entrance and entering the wood passes up into the stem."

The lesions may be very superficial, being confined to the epidermis and outer portions of the cortex, or they may be very deep, extending into the woody portion of the root or stem. The fungus generally can be isolated with ease from the tissue immediately surrounding these lesions.

Fig. 4. Tap roots of tomato plants, San Jose Canner variety, showing lesions developed by the parasite at the point of entrance. Note the discoloration of the woody elements at the cut surfaces of the secondary roots. *Verticillium* was isolated in pure culture from the tissue of the cortex in the immediate vicinity of the lesions shown in this picture. (Photograph, natural size.)

Pathologic Histology

If longitudinal or cross-sections are made of stems and roots of any plant suffering from *Verticillium* hadromycosis, the xylem will be found to be discolored. The sections may present merely a speckled or stippled appearance or the discoloration may be even and continuous (figs. 5 and 6). The discoloration varies with the host involved from brown to brownish-black, brownish-red, grey, yellow, or green. The discoloration develops soon after the invasion of the xylem by the parasite, which gains entrance to the plant through the roots. The discoloration is faint at first, intensifying as the disease runs its course, and it may be traced from the roots to the pedicels of the uppermost leaves at the tips of the plant in advanced cases.

Generally the fungus mycelium may be found in the discolored tracheae and tracheids but not always. Discoloration of the vessels in the tips of the affected plants may precede the actual penetration of the fungus into these parts (Reinke and Berthold, 164; Pethybridge, 149; Dowson, 64; and author's observations). This fact frequently renders isolation of the fungus uncertain. Material for culture purposes should be taken from the lower parts of the stems or roots of affected plants rather than from the tips.

All of the vessels of the xylem may be invaded, thus presenting a discolored ring in cross-sections, or the fungus may be sharply confined to comparatively few vessels on one side of a stem only. With certain bush fruits, such as the raspberry, a single cane or portion of a cane alone may show the discoloration.

Microscopic examination of the discolored tissue reveals the presence of mycelium in the lumina of the vessels of the xylem (plate 2, figs. 2 and 3). Both the pitted and spiral tubes are involved. The mycelium grows from below upward, and in advanced cases of the disease may be traced in an unbroken line from the roots to the tips of the plants. It is colorless at the growing tips, becoming dark brown with age. Discoloration of the vessels is due in part to the presence of this brown mycelium and to a chemical discoloration of the walls by products of the parasite.

In the vessels, the mycelium may vary in amount from a few scanty threads to a dense bundle which virtually forms a plug. The latter condition is distinctly the exception rather than the rule, however. The growth of the hyphae is generally in a longitudinal direction rather than lateral, although some branching does occur. Klebahn (113) with special staining methods determined that the myce-

Fig. 5. Characteristic discoloration developed in the wood of apricot severely affected with *Verticillium* hadromycosis. *Verticillium* sp. was isolated in pure culture from the specimen shown in this picture. (Photograph, natural size.)

lium was frequently denser in the unlignified portions surrounding the vessels than in the lumina themselves. The degree of wilt does not necessarily depend upon the amount of mycelium in the ducts; plants suffering from the disease in aggravated form may be found with comparatively little mycelium in the ducts and vice versa.

While the affected stem is still green the fungus confines itself exclusively to the water ducts, only occasionally invading cells immediately contiguous to the bundles. The pith and cambium and the cortex, including epidermis, collenchyma and bast fibers, remain perfectly healthy. As the disease increases in severity the phloem not infrequently shows necrosed areas, brown in color. (Klebahn, 113; Dufrenoy, 71, 72, and author's observations). Reinke and Berthold (164) traced the fungus even into epidermal hairs.

In the cells immediately contiguous to the infected vessels the nuclei assume an amoeboid appearance, but the cytoplasm of such cells generally appears normal and even when infiltrated with mycelium presents a well-defined chondriome. When the infection is generalized in the cells of the medullary rays, the cambium, or the bark, those cells adjoining the infected cells, still healthy, conserve their mitochondria and plastids (Dufrenoy, 68, 69).

In the leaves, the disease picture is analagous to that seen in the stems. The infection may be sharply localized or it may involve the entire organ. In some instances only a lobe of a leaf or only one leaflet of a compound leaf may become diseased.

Examination of the wood vessels in the leaves reveals the fungus in various amounts. Sudden wilting or collapse of a blade takes place only when the fungus, having pierced the vessels of the ribs at some unlignified point, penetrates the mesophyll, and not before, according to van der Lek (190) and Klebahn (113). Leaves may die in advance of actual penetration of the leaf tissue by the fungus for other reasons, however, possibly due to decreased water supply occasioned by the stoppage in the vessels lower down or to toxic substances excreted by the parasite and carried upward in the sap stream.

Van der Lek (190) described wedge-shaped necroses in cucumber leaves formed as the result of an invasion of the mesophyll by the fungus from the midrib or main veins at various points. Klebahn (113) told how the fungus penetrates in and around the loose spongy cells of the mesophyll of dahlia leaves and also described the shrinking of the palisade parenchyma.

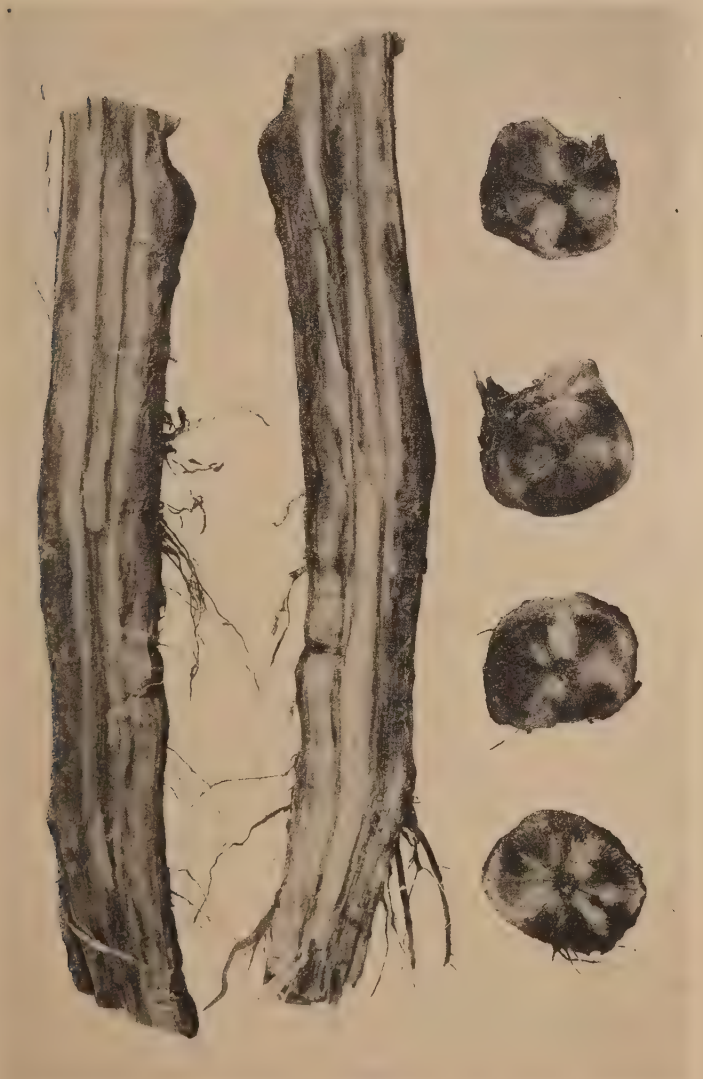

Fig. 6. Characteristic discoloration developed in the main stem of a tomato plant seriously affected with *Verticillium* hadromycosis. The fungus was isolated in pure culture from this specimen after this picture was made. (Photograph, natural size.)

Dowson (62, 64) subjected palisade and mesophyll cells scraped from a healthy michaelmas daisy leaf to a filtered liquid culture medium in which the parasite had previously been growing. Under the microscope, the chloroplasts appeared to be affected first. They migrated to either end of the cell where they eventually lost their green color. Finally they disintegrated into a bright yellow mass as the cell itself began to plasmolyze. Since he was able to produce typical symptoms in healthy stems and leaves subjected to this filtrate, Dowson concluded that the process of degeneration observed in the cells under the microscope is what happens in plants suffering from the disease. Dufrenoy (72) has reported somewhat similar observations. He also noted that the chloroplasts in the leaves no longer form starch during the day.

Reinke and Berthold (164) and Klebahn (113) note that the hyphae are very thin and reduced in diameter at the point where they pass through the cell walls, but once through they swell to a much greater size.

Reinke and Berthold (164), Klebahn (113), Dowson (63, 64), Rankin (160), van der Lek (190), van der Meer (191), Pethybridge (149), and others have observed spore formation in the diseased vessels of leaves and stems, and Klebahn (113) and van der Lek (190) have observed the development of sclerotia in the mesophyll as well as in the ducts of stems and leaves. Rankin (160) reports finding the tracheae and tracheids of maple packed with sclerotia.

Tyloses.—The presence of the parasite in the vessels stimulates the production of tyloses. Van der Lek (188, 190) refers to the "abnormally heavy production of tyloses" in the vessels of the cucumber plant. Westerdijk (204) refers to tyloses in the vessels of sugar and fodder beets; Pötschke (156) in horse-radish; Pethybridge (143), Reinke and Berthold (164), Appel and Schlumberger (8), and others in potato. Dufrenoy (69, 72) and Bordas and Joëssel (34) also mention the presence of tyloses in the stems of affected plants.

Gum.—Gum-like substances, brownish in color, are frequently produced in the parasitized vessels. Czarnecki (58) reports the production of gum in the vessels of apricot; van der Meer (191, 193) in the vessels of elm, maple, and cherry; Westerdijk (204) in beets; Pötschke (156) in horse-radish; Dowson (64) in michaelmas daisy, etc.

The exact chemical nature of this gum-like substance is not clearly understood and opinions differ as to its properties. Thus Bewley (25) says the gum is washed away from sections in the ordinary staining

process, but van der Meer (191) has the following to say of the gum in cherry wood:

> The gum appeared to be insoluble in water, alcohol 96 per cent, ethyl ether, nitric acid, sulfuric acid, and potassium hydroxide (5 per cent): no solution could be detected in ether after 1½ hours, and in nitric acid and potassium hydroxide even after 24 hours. Whereas the cell walls were almost quite solved in a drop of strong sulfuric acid after a short time, the gum remained unchanged. Boiling in water had no effect, but boiling in nitric acid caused the gum to disappear. These reactions are characteristic of wound gum.

EXPLANATION OF SYNDROMAL PHENOMENA

Discoloration of the Vessels

Opinions differ concerning the cause of discoloration of the parasitized vessels; some authors refer to the discoloration as a pigment deposited by the fungus, others believe it to be due to a change in the chemical nature of the vessel lining itself. Experimental data to substantiate either of these theories are lacking. Van der Lek (188, 190) believes the fungus secretes a toxin which exercises a corrosive action on the walls of the vessels. Pethybridge (149) considers the deep discoloration observed in potato tubers and stems to consist of the fungus threads themselves, which are dark brown. He also recognizes discoloration of the cell walls independent of the fungus. Picado (155) believes the discoloration in affected plants and wilt to be due to by-products of the fungus, each distinct from the other.

Wilt and Desiccation of the Aerial Portions of the Plant

Opinions are divided between two possible theories as to the cause of these phenomena; some attribute the wilt to thrombosis, others to biochemical reactions occasioned by toxins secreted in the sap stream by the parasite.

Thrombosis.—A great many writers consider that thrombi in the vessels bring about the wilt and desiccation observed in the tops of affected plants. Thrombi may consist of mycelium, of gum-like substances, or of tyloses.

Carpenter (49) says:

> Microscopic examination of thin sections of this material shows that the vessels are plugged with mycelium of the parasite, which interferes with the conduction of moisture to the aerial portions of the plant.

Pethybridge (149) remarks that "the wood vessels may be more or less choked," and Lawrence (117) describes fungus threads so tightly packed together in the bundles as "to form a perfect plug or cork."

Klebahn (113) takes the extreme view, accepted by no other investigators, that the fungus inhabits the vessels not as a parasite but as a saprophyte, securing its nutriment from the raw materials, also from sugars in the sap, and eventually crowding the vessels to such an extent that translocation of moisture is impeded or rendered impossible. Decline and death follow as a natural consequence.

Other writers who explain the wilt and desiccation in the tops on the basis of mycelial thrombi are: Reinke and Berthold (164), Whetzel and Rosenbaum (206), Guéguen (82), Aderhold (1), Van Hook (194), Berkeley and Jackson (20), and Pethybridge (143, 148).

Among those who regard thrombi composed of gum-like substances and tyloses as responsible for wilt and desiccation in the tops is Czarnecki (58), who states: "The sudden wilting of the branches is the mechanical effect of the formation of gum in the xylem vessels and the cutting off of the water supply of the tree."

Bewley (25) takes a similar view. Pötschke (156) regards thrombi of gum and tyloses as the cause of wilt in horse-radish.

Among other workers who have reported tyloses and gum formation in the vessels of diseased plants are: van der Lek (188, 190); Westerdijk (204); van der Meer (191, 193); Dufrenoy (67, 69, 72); Dowson (64); Pethybridge (143); Appel and Schlumberger (8); and Bordas and Joëssel (34).

Very little experimental work, if any, has been done to prove the validity of the thrombosis theory. That thrombi in the vessels are responsible for the wilt and desiccation associated with the disease has been largely assumed rather than proved.

Arguments against the thrombosis theory have been advanced by van der Lek (190), van der Meer (191), Bewley (25), and many others. Most of these workers point out that actual plugging of the vessels rarely occurs. Plants suffering the most aggravated form of the disease may have very few hyphae in their vessels, whereas those plants showing only a mild attack may show a pronounced congestion.

Reinke and Berthold (164) actually believed a form of the disease to exist in potatoes in which the vessels are free of mycelium. Closer observations by these investigators would probably have revealed the presence of scanty hyphae in the ducts.

Actual wilting such as might be associated with a lack of moisture due to plugging of the ducts may be completely absent in plants

suffering a severe attack of the disease. The lower leaves of such plants may be dead or dying but the topmost leaves may be turgid and show none of the symptoms which are associated with a lack of moisture and which might be expected to occur above the point of actual stoppage in the vascular system.

Dowson (64) conducted experiments after the manner of Hutchinson[14] to determine whether simple mechanical plugging of a certain area of the xylem would cause wilting in the tops. Dowson utilized healthy privet and lilac plants. He cut wedge-shaped pieces from the shoots of these plants on alternate sides. The operation was conducted under water, and while still under water the cut surfaces were well rubbed with vaseline and bound over with tinfoil secured with a string. They were removed then from the water and returned to their original position among the bushes. There was not the slightest trace of wilting of the leaves on the cut shoots, although the conducting channels were put out of action over a considerable area by mechanical plugging.

A further argument against the thrombosis theory is found in the fact that the disease is worse normally in the spring and fall, when cooler temperatures prevail, than in midsummer, when temperatures frequently are high and when anything which might interfere with the free conduction of moisture might easily lead to serious consequences in the plant. Bewley (24, 25, 30) reports the disease in tomatoes to be worst in the cooler parts of greenhouses, especially near the doors. He associated this phenomenon with temperature relationships (see page 230).

It has been observed that at times affected plants in the field wilt during the heat of the day but recover their turgidity at night. The same is true of plants in a greenhouse when the tops are closed during the heat of the day. Such action might be construed to be the effect of an interrelation between thrombosis and excessive transpiration, but Bewley (24, 25, 30) found that while affected plants wilted at certain high temperatures, at higher temperatures they recovered, a phenomenon difficult to explain on the basis of the thrombosis theory.

A number of workers attribute the wilt and desiccation of affected plants to the combined effect of thrombosis and toxin poisoning.

Toxins.—Considerable evidence is at hand that *Verticillium,* like certain other parasitic fungi which inhabit the vessels of plants,

[14] Hutchinson, C. M. Rangpur tobacco wilt. India Dept. Agr. Mem. 1(2): 67–83. 12 pl. 1913.

secretes a toxic substance in the sap stream which is largely responsible for the syndromal characteristics of the disease.

Bewley (25) has demonstrated that a substance toxic to plants is present in liquid culture media upon which the fungus has been permitted to grow for a considerable period of time. Of his numerous experiments which he repeated several times, the following is typical:

Sterile Dox's solution containing 20 per cent saccharose was planted to *Verticillium* from tomatoes. After thirty days the medium was distinctly yellow. It was carefully filtered and diluted to three times its original bulk with sterile water to offset the effects of exosmosis which by previous experimentation had been proved to interfere with the results when the filtrate was used at its original concentration. Tomato seedlings, 5 inches in height, cut off under water near the roots, were placed in a series of flasks. The results are given in table 1.

TABLE 1

BEWLEY'S DEMONSTRATION OF TOXIN FORMATION BY VERTICILLIUM

Series	No. of flasks	Treatment	Results
I	5	Sterile filtrate	Plants wilted in 42 minutes
II	5	Sterile filtrate previously heated for 5 minutes at 100° C	Slight wilting after 95 minutes which did not increase up to 24 hours
III	5	Diluted sterile medium for controls	Unaffected
IV	5	Sterile water controls	Unaffected

The above test demonstrated the presence of a toxic substance in the filtrate. Also that heating at 100° C for 5 minutes largely destroys this substance or at least greatly attenuates it.

To 1,000 cc sterile filtrate prepared as above, Bewley added absolute alcohol until all the resultant precipitate had been thrown down. This was filtered off, pressed, and dried. A similar lot of sterile culture medium was so treated for controls. After 24 hours the two precipitates were redissolved in 3,000 cc sterile water and distributed in 300 cc flasks. Tomato plants were added as before. The results are given in table 2. This experiment further demonstrated the presence of a water-soluble, thermolabile toxic substance in the culture filtrate.

Bewley's attempt to isolate endoenzymes from crushed spores and mycelium failed.

Modifying the methods of Crabil and Reed,[15] Bewley was able to demonstrate the following enzymes: amylase, inulase, emulsin, lipase, protease, erepsin and amidase.

Dowson (62, 64) conducted experiments similar to Bewley's. He placed healthy vigorous shoots of michaelmas daisy in sterile filtrate from liquid cultures of the fungus originally isolated from michaelmas daisy. He concluded from the wilt produced that an exotoxin is excreted in the medium by the fungus.

TABLE 2

BEWLEY'S DEMONSTRATION OF THE FORMATION OF WATER-SOLUBLE, THERMOLABILE TOXINS BY VERTICILLIUM

Series	No. of flasks	Treatment	Results
I	5	Dissolved culture precipitate	Plants wilted in 72 minutes
II	5	Dissolved culture precipitate heated at 100° C for 5 minutes	Plants showed slight wilt in three hours
III	5	Dissolved culture precipitate from sterile medium	Plants not affected during 24 hours

Dowson also treated healthy, growing michaelmas daisies in situ with similar filtrate as follows: Glass tubes were drawn out to a sharp, curved point. The latter was inserted into the vascular system of a healthy plant and the tube filled with filtrate. Eight plants were so treated, but because of the formation of a gum-like substance at the point of insertion of the glass tube, which prevented the absorption of the liquid, all the tests failed but one. In this case, fifteen days after the start of the experiment, during which time the tube was filled three times with filtrate, the leaves at the point of insertion of the tube turned yellow. At the end of a month all leaves of the plant above the point of insertion of the tube had either died or turned yellow after the characteristic manner of *Verticillium* hadromycosis. The leaves below the point of insertion of the tube remained green and healthy.

Another experiment of Dowson with cells scraped from the healthy leaves of michaelmas daisy and subjected to the action of the filtrate has been briefly reported on page 222.

[15] Crabil, C. H., and H. S. Reed. Convenient methods for demonstrating the biochemical activity of microorganisms with special reference to the production and activity of enzymes. Biochem. Bul. 4(13):30–44. 1915.

Picado (155) conducted experiments similar to Bewley's. He placed flageolet bean seedlings and healthy potato shoots in sterile filtrate from month-old cultures on Richard's solution. He concluded that a definite exotoxin is excreted by *Verticillium albo-atrum* R. and B. and *V. duboys* Foëx. Also that wilting and browning of the vessels are not due to the same cause, since shoots placed in filtrate in which the exotoxin had been destroyed by heat did not wilt, but developed discoloration in the vessels, nevertheless. Suitable controls in fresh Richard's solution remained unaffected.

Picado concluded that endotoxins also exist. The total mass of mycelium obtained from a month-old culture on 250 cc of Richard's solution in 50 cc Erlenmeyer flasks was carefully triturated with washed sand. It was then permitted to autolyse in 100 cc distilled water for 4 hours, when it was filtered and different dilutions made. Bean seedlings and potato shoots submitted to the various dilutions of the extract wilted. From the results obtained, Picado concluded that endotoxins exist which are effective in dilutions as high as 1 to 15. This extract heated gave even more pronounced results in certain instances, which would indicate that a true poison was present rather than a toxin.

To find out if this phenomenon was not a case of true poisoning rather than the effect of a toxin (in the strict sense of the word) Picado proceeded as follows:

The exotoxins in month-old culture solutions were precipitated with equal amounts of absolute alcohol. The supernatant liquid was filtered off and discarded.

Next an extract from triturated mycelium was similarly treated, and the resultant precipitate filtered out. In this instance the supernatant liquid was condensed by heating at 80° C for 24 hours, at the end of which time a waxy, brownish, very hygroscopic precipitate was obtained, the dry weight of which exceeded that of the albuminoid precipitates. This material presumably was free of the thermolabile toxins and contained the thermostable poison.

In a series of graduated dilutions of these various precipitates, Picado placed bean seedlings and potato shoots as before. The dilutions of the poison-containing material were heated at 100° C for 5 minutes before the experiment. He found that this heated extract was at least four times more pathogenic for potatoes than the exotoxin or endotoxin-containing solutions. His experiments might indicate that lysis from poisons as well as toxins occurs when plants are attacked by *Verticillium*.

From his experiments, Picado further concluded that the effect of endotoxins and exotoxins on plants not attacked by *Verticillium* may be considerably different from that on plants which are natural hosts to the parasite.

Dufrenoy (71, 72, 320) believes the fungus reduces nitrates to nitrites and that the latter exert a toxic effect on the plant. He placed healthy apricot shoots in 1 per cent solutions of sodium nitrate and sodium nitrite. The foliage on the stems in the nitrite solution was badly wilted whereas that on the stems in the nitrate solution remained unaffected. Bordas and Joëssel (34) also concluded from their experiments with the fungus in vitro that it exerts a strong reducing action on its substrate, and that among these reduction products are nitrites, which may be responsible for the wilt.

Among other workers who believe toxins to be responsible largely for the wilt phenomena are van der Lek (188, 190), Appel and Schlumberger (8), Lawrence (117), and Rankin (159).

THE METHOD OF ATTACK BY THE PARASITE

With very few exceptions, writers are agreed that the disease is contracted through the root systems of susceptible plants. Opinions differ, however, as to the ability of the fungus to attack sound, healthy roots. Reinke and Berthold (164), the first to establish the etiology of the disease, clearly demonstrated the ability of the fungus to penetrate healthy root tissue. The recent work of several investigators has independently confirmed Reinke and Berthold's views. Evidence that the fungus is dependent upon wounds for means of entrance has been assumed, largely, by the many writers who advance this theory, rather than established as fact by investigational data.

Reinke and Berthold (164) were unable to secure infection of the uninjured roots of potato plants grown in humid chambers by means of spores, because the spores did not germinate. When bits of mycelium from cultures were placed upon uninjured roots growing under similar conditions, infection quickly took place. At the point of entrance of the fungus a brown lesion developed. Two days after the start of the experiment the root began to turn back at this spot. Examination of the tissues revealed the presence of the fungus in abundance in the cells beneath the epidermis. These investigators were fully convinced that the fungus is capable of penetrating healthy uninjured root tissue.

Van der Lek (190) conducted similar experiments with uninjured roots and found them to be attacked readily. Microscopic examination revealed the fungus within the tissues. This writer points out that the origin of the roots of tap-rooted plants is not at the surface of the tap root but deep in the tissue in the pericycle; this fact affords easy entrance to the vascular structure of the plant stem after the parasite has gained entrance to the lateral root.

Van der Meer (191) carefully disinfected the surface of cucumber seeds and potato tubers and germinated them under asceptic conditions. When the root systems were well developed, *Verticillium* spores in aqueous suspension were introduced in the tubes in which the plants were growing. The roots were attacked, and the points of entrance of the fungus were characterized by small brown spots. Microscopic examination revealed mycelium within the tissues. Cultures made from the diseased tissues established its identity. The roots were attacked either directly through the epidermal cells or through the root hairs.

She also noted cone-shaped protuberances or callus-like structures on the inner walls of parasitized cells directly opposite the point of penetration of the fungus. Their significance has not been explained, but they may be defense structures developed by the plant. They are ineffectual, however; the fungus makes its way through them. Dufrenoy (68) reported similar structures in the parenchyma cells of pea seedlings inoculated with *Verticillium* from apricot.

Bewley (25) grew tomato seedlings in flasks of Czapeck's synthetic nutrient agar, and when the root systems were well developed he added a spore infusion of *Verticillium albo-atrum*. The healthy roots were readily attacked and wilt occurred nine days later.

ECOLOGY

Temperature Relations.—That *Verticillium* hadromycosis is primarily a disease of cool regions in contradistinction to *Fusarium* hadromycosis, which is favored by warmer temperatures, is universally agreed by writers, among whom may be mentioned Bewley (24, 25, 28, 30), Brittlebank (36), Edson and Shapovalov (75), McKay (129), Rudolph (168), Shapovalov and Link (176), Taylor (185), van der Meer (191), and Wollenweber (213, 216).

Wollenweber (213) has pointed out rightly that *Verticillium* hadromycosis rarely makes its appearance in the United States below the thirty-fifth degree of latitude. It has been recognized definitely,

however, in all but one of the coastal counties in California below this latitude, also in Alabama (49). Although generally confined to the coastal counties of California, it is known to occur in the warmer interior counties of the San Joaquin and Sacramento valleys, where it occasions appreciable damage at times.

The minimum, optimum, and maximum temperatures at which the disease may be expected to occur, as well as those at which the parasite may be expected to grow in culture, are given in table 3.

TABLE 3

TEMPERATURE RELATIONS OF VERTICILLIUM SPP.

Author	Species	Degrees Centigrade		
		Minimum	Optimum	Maximum
In Plants				
Bewley (25, 26, 29, 31)	*V. albo-atrum*	15.6	21.2–22.8	24
Schoevers (175)	*V. albo-atrum*	.....	.....	25
Bennett (16)	*V. ovatum*	.....	27–32	.. .
In culture				
Bewley (25, 26, 29, 31)	*V. albo-atrum*	4.4	23.3	30
Pötschke (156)	*V. albo-atrum*	5–10	28	33–37
Czarnecki (58)	*V. species*	10–14	20–25	35–37
Chaudhuri (50)	*V. albo-atrum*	10	22–5	27
Edson and Shapovalov (75)	*V. albo-atrum*	5	25	30–35

It will be seen from table 3 that the optimum temperature for the greatest development of the disease in plants closely approximates that of the optimum temperature for growth of the parasite in culture.

The optimum temperature for development of the disease in raspberries as given by Bennett (16) is probably an error. This temperature is distinctly above that generally recognized as favorable to *Verticillium* hadromycosis. Similarly, the optimum temperature given by Pötschke (156) for growth of *Verticillium albo-atrum* in culture is probably an error, since it is much higher than that found by several other workers.

Chaudhuri (50) used smaller differences in temperature in his studies than Czarnecki (58) or Edson and Shapovalov (75). Had Edson and Shapovalov used smaller differences in temperature also, in all probability their figures for the optimum temperatures would have coincided more closely with those of Chaudhuri.

Chaudhuri (50) points out that to determine temperature relationships by the rate of spread and size of the colony is not as simple as it appears. He found that several factors materially influence the results of his experiments, namely, the depth to which the culture medium is poured in the plates, the kind of medium used, the extent of aeration in the plates, etc.

It would be unwise to devote further space here to the considerable amount of cultural studies that have been reported, because of the existing confusion in the taxonomic status of the several putative species of *Verticillium* associated with the disease. For instance, Chaudhuri (50) and Bewley (24, 25, 28, 30) have reported in detail the results of their cultural studies of *Verticillium albo-atrum* R. and B., as have Pethybridge (149) and van der Meer (191). But in studying the data, it is only too obvious that the first two workers were working with strains of the fungus which were not identical with that studied by the latter two.

Bewley (24, 25, 28, 30, 317) found that wilted cucumber plants recovered their turgidity when subjected to shade and temperature of 25° C. Also that the permanency of this recovery was dependent upon the length of time at which the plants were subjected to this temperature. Table 4 gives the results reported in 1928.

TABLE 4

Influence of High Temperatures on the Recovery of Verticillium-Infected Cucumber Plants*

Number of wilted plants	Length of time in shaded cucumber house; average temperature 25° C	Effect of high temperature	Length of time after returning to average temperature of 20° C before plants again wilted
	days		
12	1	Recovered	15 hours
12	2	Recovered	15 hours
12	7	Recovered	2 days
12	14	Recovered	3 days
12	30	Recovered	16 days
12	75	Recovered	30 days

*From: Bewley, W. F.; Diseases of glasshouse plants, 208 pp. Ernest Benn, London, 1928.

It is seen that when the higher temperature is operative for a short time only, the recovery is not a lasting one, and the wilt symptoms again appear. Longer exposure to high temperatures produces

a more lasting result, for after 75 days at 25° C, the plants remained turgid for 30 days at a temperature favorable to wilt.

Pethybridge (150, 151) succeeded in disinfecting diseased potato tubers by heating them without impairing their value for seed purposes. See "Control of *Verticillium* Hadromycosis of Potato Tubers by Heat" (page 284).

Shade.—Bewley (24, 25, 28, 30) subjected cucumber plants in all stages of the disease to a temperature of 25° C in a greenhouse. Part of the plants were shaded and part were not. His results are given in table 5.

TABLE 5

INFLUENCE OF SHADE ON THE RECOVERY OF VERTICILLIUM-INFECTED CUCUMBER PLANTS

Number of wilted plants	Days wilt had been visible prior to experiment	Per cent recovered in shaded cucumber house, average temperature 25° C	Per cent recovered in unshaded cucumber house, average temperature 25° C
20	2	100	100
20	7	100	100
20	14	100	100
20	21	100	90
20	30	100	80

Bewley comments on the experiment as follows:

All the plants recovered in the shaded house, but only a percentage recovered in that which was not shaded. The plants which did not recover in the unshaded house, being badly wilted ones, were probably desiccated before they had a chance to recover.

These observations appear to justify the conclusion that temperature is a most important factor, while shading is valuable because it assists the plant by reducing transpiration . . . . so that the toxic products excreted by the fungus are not carried up the plant in such large amounts (30).

Van der Lek (190) has reported favorable results of shade on tomatoes in greenhouse experiments and attributes same to reduced transpiration.

Moisture Relations.—Opinions are varied, but most writers regard drought as distinctly favorable to the disease (van der Lek 190; Haenseler 83; van der Meer 191; and others). However, some writers feel that the disease is more prevalent in wet seasons or on wet ground; an anonymous writer (4) reports sweet cherries to be seriously affected on low water-logged ground in Czecho-Slovakia. Blattný (32) says the horse-radish suffers worst in damp years. Dowson (64) believes moisture leads to a more rapid and fatal attack in asters. Bewley (24, 30) reports that heavy watering aggravates the wilt in tomatoes.

Van der Meer (191), infected potato plants in pots with *Verticillium dahliae*. One set of plants was kept moist under glass, a second set was watered every day and a third set was placed in a penthouse and kept as dry as possible. The third set was affected much worse by the disease and its development was much more rapid than in plants kept moist.

In California, serious outbreaks of the disease have been observed both in plants suffering severely from drought and in those growing in an abundantly watered soil. Large raspberry patches in low, heavily watered soil have been rendered so unprofitable by the disease that their cultivation was no longer possible. On the other hand the disease may assume serious epidemic proportions in tomato fields in which the plants have been subject to drought conditions. Severe outbreaks of the disease have been observed in prune, peach, and apricot orchards, subjected to the widest extremes of soil moisture. In California the disease may assume serious epidemic proportions one year but be virtually absent the year following. With cultural and soil conditions remaining the same on the ground where this phenomenon has been observed, I am inclined to believe an additional factor, possibly one of temperature, is necessary to permit generalized infection of susceptible crops to take place.

Soil.—Opinions are divided sharply as to which soil types are most conducive to the development of the disease and the propagation of the fungus.

Van der Lek (188, 190), Pethybridge (148), Weimer (203), Wollenweber (216), Spieckermann (181), Quanjer (158), and others regard loams and sandy loams as favorable to the disease. Utkin (186) and Blattný (32) consider the disease worst on heavy sandy loams.

Many writers agree that a high content of manure, compost, humus or other organic matter in the soil is conducive to the spread and propagation of the fungus (van der Lek, 190; Pethybridge, 149; Haenseler, 84; Schoevers, 175; Bewley, 24, 25, 28, 30; Brittlebank, 36; Utkin, 186; Blattný, 32).

Bewley (24, 25, 28, 30) is inclined to think that the organic content is a greater factor than the soil type in aiding in the propagation of the fungus.

He considers clay soils, which, by virtue of their greater water-holding capacity are cooler soils, to be favorable to the development of the disease. Van der Lek (190) also regards clay, as well as sedimentary soils, as favorable to the development of the disease.

Sherbakoff[16] reports the disease to be common in cotton growing along the Mississippi River on 'gumbo' soils.

Haenseler (91) reports the disease in egg plant to be less severe on acid soils.

Bewley (30) experimentally proved sterilized soil to be more conducive to the rapid spread of the fungus than unsterilized soil.

In California the disease has been observed in severe epidemic form on soils varying from a light sandy loam to a heavy clay and adobe types.

REPORTS OF CROSS-INOCULATION EXPERIMENTS WITH VERTICILLIUM SPECIES

Successful Cross Inoculations.—Many references occur in the literature to successful cross-inoculation experiments with strains of *Verticillium* isolated from plants suffering from hadromycosis. These results are summed up in table 6.

Bewley (30) reports the potato, tomato, cucumber, melon, sweet pea, snapdragon, and elm to be subject to infection by *Verticillium albo-atrum* from any one of these same hosts. Also, he was able to infect eggplant, *Capsicum* sp., cotton, and sycamore maple with *Verticillium albo-atrum* from tomato (24, 25, 28).

Van der Lek (189) infected potatoes with *Verticillium albo-atrum* from melons, cucumbers, and tomatoes, and vice versa.

Carpenter (47, 49) infected okra with *Verticillium albo-atrum* from okra, potato, eggplant, and snapdragon; also eggplant with the fungus from okra, snapdragon, and eggplant; and cotton with *Verticillium* from okra.

Jagger and Stewart (110) infected barberry with *Verticillium* sp. from eggplant and vice versa. Maple was successfully inoculated with *Verticillium* from barberry and eggplant; eggplant was successfully inoculated with *Verticillium* from potato.

Haenseler (90, 94) infected eggplant with *Verticillium albo-atrum* from peach and maple. Weimer (203) infected eggplant with *Verticillium albo-atrum* from udo.

Dufrenoy (72) infected peas with *Verticillium dahliae* Kleb. from apricot.

[16] In 1929, C. D. Sherbakoff briefly described the disease in cotton. (Phytopath. 19(1):94. 1929. Univ. Tennessee Agr. Exp. Sta. Cir. 24:2. 1929.) In the article in Phytopathology, an attempt to distinguish between cotton wilt due to *Fusarium vasinfectum* and that due to *Verticillium albo-atrum* has been made. The descriptions are contradictory, however, particularly with reference to the discoloration observed in the affected plants.

TABLE 6

INTERHOST RELATIONSHIP OF VERTICILLIUM SP. ESTABLISHED BY CROSS-INOCULATION EXPERIMENTS OF VARIOUS WORKERS

Verticillium sp. from	Verticillium sp. to: Acer pseudoplatanus L.	Acer rubrum L.	Aconitum napellus L.	Antirrhinum sp.	Berberis thunbergii D.C.	Capsicum sp.	Cherry	Cucumis melo L.	Cucumis sativus L.	Eschscholtzia californica Cham.	Gossypium herbaceum L.	Hibiscus esculentus L.	Lathyrus odoratus L.	Lupinus polyphyllus Lindl.	Malva rotundifolia L.	Medicago hispida Gaertn.	Papaver rhoeas L.	Phlox decussata Hort.	Prunus armeniaca L.	Prunus cerasifera Ehrh.	Rubus idaeus L.	Senecio vulgaris L.	Solanum lycopersicum Trn.	Solanum melongena L.	Solanum tuberosum L.	Taraxacum officinale Weber	Ulmus sp.
Acer platanoides L.																								X			
Acer sp.																								X			
Aconitum napellus L.														X									X		X		
Antirrhinum sp.								X	X			X	X										X	X	X		X
Aralia cordata Thunb.																								X			
Aralia racemosa L.																								X			
Berberis thunbergii D. C.		X																						X			
Cherry			X						X					X				X					X		X		
Cucumis melo L.				X					X				X										X		X		X
Cucumis sativus L.				X				X					X	X				X					X		X		X
Hibiscus esculentus L.												X												X			
Humulus lupulus L.																									X		
Lathyrus odoratus L.				X				X	X														X		X		X
Lupinus polyphyllus Lindl.			X				X											X					?		X		
Miscellaneous sources																X	X										
Papaver rhoeas L.			X											X				X					X		X		
Phlox decussata Hort.			X											X									X		X		
Prunus armeniaca L.				X									X			X				X	X	X	X				
Prunus mahaleb L.			X				X		X					X				X		X			X		X		
Prunus persica Sieb. & Zucc.																				X	X		X	X			
Rhus canadensis Marsh.																							X	X			
Rubus idaeus L.										X					X	X				X	X	X	X				
Solanum lycopersicum Trn.	X		X	X		X	X	X	X		X	X	X	X	X	X		X	X	X	X		X	X	X		X
Solanum melongena L.		X			X							X							X					X			
Solanum tuberosum L.			X	X				X	X				X	X				X					X	X			X
Ulmus sp.				X				X	X				X										X		X		

Wormald (225) reports the successful inoculation of potatoes with *Verticillium* sp., from hops.

Van der Meer (191) successfully inoculated *Aconitum napellus* L. with *Verticillium dahliae* Kleb. from *Prunus mahaleb*, *Lupinus polyphyllus* Lindl., *Phlox decussata* Hort., *Papaver rhoeas* L., *Solanum tuberosum* L., and with *V. albo-atrum* R. and B. from *Solanum lycopersicum* Trn., and cherry; also *Lupinus polyphyllus* Lindl. with *Verticillium dahliae* from *Prunus mahaleb*, *Aconitum napellus* L., *Phlox decussata* Hort., *Papaver rhoeas* L., *Solanum tuberosum* L. and with *Verticillium albo-atrum* from *Solanum lycopersicum* Trn., *Cucumis sativus* L. and cherry.

In experiments reported in the same paper (191), *Phlox decussata* Hort. was infected with *Verticillium dahliae* from *Prunus mahaleb* L., *Lupinus polyphyllus* Lindl., *Aconitum napellus* L., *Papaver rhoeas* L., and *Solanum tuberosum* L., and with *Verticillium albo-atrum* from *Solanum tuberosum* L., *Solanum lycopersicum* Trn., *Cucumis sativus* L., and cherry.

Solanum tuberosum was infected with *Verticillium dahliae* from *Prunus mahaleb* L., *Lupinus polyphyllus* Lindl., *Aconitum napellus* L., *Phlox decussata* Hort., and *Papaver rhoeas* L., and with *Verticillium albo-atrum* from *Solanum lycopersicum* Trn., *Cucumis sativus* L., and cherry.

Cherry was infected with *Verticillium dahliae* from *Prunus mahaleb* L., and *Lupinus polyphyllus* Lindl., and with *Verticillium albo-atrum* from *Solanum lycopersicum* and *Cucumis sativus* L.

Solanum lycopersicum Trn. was infected with *Verticillium dahliae* from *Prunus mahaleb* L., *Lupinus polyphyllus* Lindl. (?); *Aconitum napellus* L., *Phlox decussata* Hort., *Papaver rhoeas* L., and *Solanum tuberosum* L., and with *Verticillium albo-atrum* from *Solanum tuberosum* L., *Cucumis sativus* L., and cherry.

Cucumis sativus L., was infected with *Verticillium albo-atrum* from *Solanum tuberosum* L., *Solanum lycopersicum* and cherry.

M. F. Barrus of the New York College of Agriculture successfully inoculated eggplant with *Verticillium* sp. from *Aralia racemosa* L., *Rhus canadensis* Marsh. and *Acer platanoides* L. Also tomato with the fungus from peach and *Rhus canadensis*.[17]

I successfully inoculated California poppy (*Eschscholtzia californica* Cham.), bur clover (*Medicago hispida* Gaertn.), dandelion (*Taraxacum officinale* Weber), and groundsel (*Senecio vulgaris* L.) with *Verticillium* from raspberry; *Senecio vulgaris* L. with *Verticil-*

[17] Personal letter.

lium from apricot; Shirley poppy (*Papaver rhoeas* L.) with mixed cultures of *Verticillium* not from poppy; *Medicago hispida* Gaertn. with *Verticillium* from apricot and tomato; common mallow (*Malva rotundifolia* L.) with *Verticillium* from tomato and raspberry.

I have infected myrobalan seedlings with *Verticillium* from peach, raspberry, apricot and tomato; apricot seedlings with *Verticillium* from tomato; tomato plants with *Verticillium* from peach, apricot and raspberry; raspberry plants with *Verticillium* from apricot, peach and tomato.

Unsuccessful Cross-Inoculation Experiments.—Haenseler (90) was unable to infect peach seedlings or peach twigs with *Verticillium* from okra, eggplant, or peach, nor was he able to produce the disease in healthy peach twigs by budding them with buds from slightly diseased peach twigs. The details of his experiments or the number of inoculations made are not given in his paper.

M. F. Barrus of the New York College of Agriculture was unable to infect castor bean or pepper plants with *Verticillium* sp. from *Aralia racemosa* L., *Rhus canadensis* Marsh, *Acer platanoides* L. or peach.[18] The details of his experiments have not been published.

Jagger and Stewart (110) were unable to infect eggplant and barberry with *Verticillium* from maple, or maple with *Verticillium* from potato. Their experiments are open to criticism because too few plants were used.

Haenseler (84) was unable to infect tomato and pepper plants with *Verticillium* isolated from eggplant. The details of his experiments and the number of plants used are not given in his paper.

Van der Meer (191) was unable to infect *Cucumis sativus* L. with *Verticillium dahliae* Kleb. from *Prunus mahaleb* L., *Lupinus polyphyllus* Lindl., *Aconitum napellus* L., *Phlox decussata* Hort., *Papaver rhoeas* L. or *Solanum tuberosum* L. She was able to infect *Cucumis sativus* L. with *Verticillium albo-atrum* R. and B. from *Solanum tuberosum* L., however.

She was unable to infect *Aconitum napellus* L. with *Verticillium albo-atrum* from *Solanum tuberosum* L. or *Cucumis sativus* L., but was able to infect *Aconitum napellus* L. with *Verticillium dahliae* from *Solanum tuberosum* L.

She was unable to infect cherry with *Verticillium dahliae* from *Aconitum napellus* L., *Phlox decussata* Hort., and *Papaver rhoeas* L.

Van der Meer's experiments are open to criticism because too few plants were used. In none of her experiments were more than four

[18] Personal letter.

plants used, and generally only one or two plants were inoculated with any given strain.

The general impression obtained from reports of unsuccessful cross-inoculation experiments is that the writers used too few plants.

That infection of susceptible plants by *Verticillium* from the same species or from different sources is dependent on outside factors not too well understood, is generally agreed by writers. For this reason the failure to obtain infection in cross or direct inoculation experiments by the writers referred to above should not be considered final by any means. It is well known that *Verticillium* hadromycosis may be exceedingly prevalent and severe one year in orchards and fields of truck crops and bush fruits and virtually absent in these same crops on the same ground the next. Haenseler (90) concluded, from the difficulty he experienced in infecting peach with *Verticillium* from peach, that "very special conditions for infections" are required. Similarly, Bewley concluded from his experiments that there exists "an intimate relation between temperature and successful inoculation results" (24). Reinke and Berthold (164), Klebahn (113), Lindfors (119), and many others have remarked upon the refractory results obtained in their inoculation experiments with *Verticillium*.

At the Deciduous Fruit Field Station in 1924, over 250 inoculations were made on twigs of healthy apricot trees with *Verticillium* from apricot, tomato, peach and raspberry. Stab and flap wounds were made after the bark had been sponged with denatured alcohol. The wounds were not made until the bark was perfectly dry. In some instances the wounds were bound up with moist, sterile bandages after the inoculations had been made. In other cases the wounds were left exposed. The inoculum used consisted of masses of sclerotia, spores, and mycelium scraped from pure cultures of the fungus growing on Czapeck's synthetic nutrient agar. Not more than a total of 5 of these inoculations were successful. *Verticillium* from raspberry and tomato produced definite streaking in the wood, and the fungus was recovered at a distance of several inches away from the point of inoculation. The *Verticillium* originally obtained from diseased apricot did not attack the apricot under the conditions of the experiments.

In another experiment nearly 300 inoculations were made in the canes of healthy Ranere raspberry plants with *Verticillium* from the sources already given. In addition to stab and flap wounds in the canes, fully 50 stab inoculations were made below the ground in the roots. Also, about 50 inoculations were made in the canes as follows: Freshly cut, thin sections of diseased apricot wood were inserted in

slits made in the canes. Some of the inoculations were covered with moist, sterile bandages and others were left exposed. None of the inoculations on raspberry plants were successful that year. It was concluded that conditions were not right at the time the inoculations were made to permit of infection. The temperatures may have been too high, since the inoculations were made in May and June. Many investigators regard summer temperatures as unfavorable to the development of the disease. In subsequent years, successful cross inoculation of the raspberry was obtained, and these experiments are reported in the following section.

EXPERIMENTS AT THE DECIDUOUS FRUIT FIELD STATION

The cultural similarity of the *Verticillium* isolated from stone fruits, bush fruits, and truck-crop plants in California led to cross-inoculation experiments to establish the identicalness of the organism in these three distinct groups. Myrobalan seedlings and raspberry and tomato plants were selected as representative of the three groups and most suited to cross-inoculation purposes.

Tomato.—Tomato seed, varieties San Jose Canner and Stone, were soaked for one hour in a disinfectant solution consisting of 5 parts formalin, 40 per cent strength, in 500 parts water, and then planted in flats of soil previously sterilized by steam in an autoclave at 60 lbs. pressure for one hour. When the plants were about 6 inches high they were transferred to pots of soil which had been steam sterilized like the flats. One plant was placed in each pot. When the plants were about 12 inches high, the soil in each pot was inoculated with *Verticillium* from mono-sporic cultures on sterilized string beans in glass tubes or on Czapeck's synthetic nutrient agar. A blunt steel rod about the diameter of an ordinary lead pencil was dipped in alcohol, flame sterilized, and then pressed deep into the damp soil immediately contiguous to the plant. Into the hole thus produced, a liberal amount of the inoculum was introduced, care being taken to disseminate the fungus into all parts of the hole. The hole, which usually was quite filled with the inoculum, was pinched shut at the surface of the ground. Controls were prepared in a similar manner, but no inoculum was used. Characteristic symptoms of the disease were observed in all plants in the inoculated pots by the ninth day. The plants remained small, the leaves assumed a dull appearance and

showed the characteristic rolling at the margins and purpling of the veins. The controls eventually grew to as much as three times the size of the inoculated plants and were healthy to all appearances (fig. 7). Cultures were made from both the controls and the inoculated plants. See table 7 for results.

Fig. 7.—Cross-inoculation experiments with tomato. All plants are of the same age. The two pots on the left are controls.

The soil in the third pot from the left was inoculated with a pure culture of *Verticillium* sp. from apricot; the fourth with a pure culture of *Verticillium* sp. from tomato, and the fifth with a pure culture of *Verticillium* sp. from raspberry. The fungus was recovered from the plants in the inoculated pots from a point in the stems high above the ground level.

TABLE 7

CROSS-INOCULATION EXPERIMENTS WITH TOMATOES

Mono-sporic culture of *Verticillium* from	Variety of tomato plants used	Total number plants used	Number of inoculated plants		
			Yielding *Verticillium* in culture	Yielding miscellaneous organisms other than *Verticillium*	Yielding no organisms in culture
Tomato	San Jose Canner	42	13	17	12
	Stone	6	6	0	0
Apricot	San Jose Canner	44	12	15	17
	Stone	40	10	1	29
Raspberry	San Jose Canner	61	28	5	28
	Stone	23	14	2	7
Peach	San Jose Canner	49	22	20	7
	Stone	36	18	7	11
Controls (no inoculum used)	San Jose Canner	61	0	0	61
	Stone	27	0	0	27

TABLE 8

CROSS-INOCULATION EXPERIMENTS WITH RANERE RASPBERRY

Mono-sporic culture of *Verticillium* from	Total number Ranere raspberry plants used	Number of inoculated plants	
		Yielding *Verticillium* in culture	Yielding no organisms or organisms other than *Verticillium*
Tomato	10	4	6
Apricot	10	10	0
Raspberry	10	5	5
Peach	10	6	4
Controls (No inoculum used)	40	0	40

Raspberry.—Two hundred and fifty healthy Ranere raspberry bushes were planted at the Deciduous Fruit Field Station, which was then located at Mountain View, California. The soil was free of *Verticillium.* During the early spring the second year after planting, healthy young shoots, perhaps 6 inches in height, were carefully separated from the parent bushes and planted in pots of clean soil. When the plants had become fully established in the pots, the soil was inoculated with *Verticillium* in the manner described above for tomatoes. Controls of the same type were also provided. Table 8 gives the results obtained the first year of the experiments.

The experiment was repeated the following year on a much larger scale. In the late fall of the same year symptoms of the disease were apparent in the majority of inoculated plants. All plants, including the controls, were taken up, and cultures were made from them. The results were lost owing to the unfortunate mistake made by a new assistant. Freshly prepared but unsterilized Czapeck's synthetic nutrient agar was used to make the cultures from the large number of plants used in this experiment. Before the fungus possibly present in the material could grow, the surface and body of the culture medium in each tube was so densely overrun with bacteria and moulds that growth of *Verticillium* was impossible.

Myrobalan Seedlings.—Myrobalan seed from healthy trees were stratified in clean sand and the young plants transferred after germinating to pots of soil previously sterilized in the autoclave with steam at 60 lbs. pressure for one hour. One seedling was placed in each pot. When the plants were about 12 inches tall, the soil was inoculated with *Verticillium* in the manner described for tomatoes. See table 9 for results.

TABLE 9

CROSS-INOCULATION EXPERIMENTS WITH MYROBALAN SEEDLINGS

Mono-sporic culture of *Verticillium* from	Total number myrobalan seedlings used	Number of inoculated plants	
		Yielding *Verticillium* in culture	Yielding no organisms or organisms other than *Verticillium*
Tomato	15	11	4
Apricot	21	4	17
Raspberry	25	9	16
Peach	22	9	13
Controls (No inoculum used)	25	0	25

Apricot Seedlings.—It was planned to use apricot seedlings as well as myrobalan seedlings in the cross-inoculation experiments. The apricot seed germinated poorly, and the young plants did not thrive under the conditions of the experiment. The experiment was abandoned, but not before several apricot seedlings inoculated with *Verticillium* from tomato had become seriously diseased. The fungus was recovered from the affected plants by cultural methods.

Mature Apricots.—Twigs of healthy, mature apricot trees were inoculated with *Verticillium* from raspberry, tomato, apricot, and peach. In several instances the twigs became infected, and the fungus was recovered from the discolored wood several inches above the point of inoculation. Infection with *Verticillium* from raspberry and tomato alone was obtained. These experiments have been described on page 239 of this paper.

Method of Making Cultures.—Material for culture purposes was invariably taken from the main stem of the plant at least 2 inches above the surface of the soil and generally from that part of the wood showing the characteristic discoloration of the disease. Several cultures were made from each plant.

The stems were cut into 2-inch lengths, washed with mercuric bichloride, 1/1000, for 5 minutes and then rinsed with sterile water. Plantings were taken with a flame-sterilized knife and imbedded in Czapeck's synthetic nutrient agar slants, the usual precautions being taken to avoid contamination.

Cultures were also made from all check plants, but in no instance was *Verticillium* isolated.

DISCUSSION OF VERTICILLIUM SPECIES ASSOCIATED WITH HADROMYCOSIS

Since Reinke and Berthold (164) first described *Verticillium alboatrum* on potato, a number of new species of *Verticillium* reported to be the cause of hadromycosis have been described. The disease has been attributed also to several species of *Acrostalagmus,* but this name is now abandoned, since it is generally agreed that this genus is identical with *Verticillium.*

In studying the descriptions of these various species of *Verticillium* and *Acrostalagmus* one is struck by the similarity existing between them. For the most part claim to specific rank is based upon very slight morphological differences. Frequently the descriptions have been made from cultures on artificial media.

It is not sufficiently appreciated by many investigators that morphology alone is inadequate as a sole means of distinguishing between species. This is particularly true of fungi growing on artificial culture media; unless a number of important factors are considered and due allowance made for them (which only too frequently is not done) marked changes may occur in the characteristics of an organism, which are not of a permanent nature and may lead to mistakes in taxonomy. The kind of medium, its acidity or alkalinity, the depth to which it is poured in the plates, the extent of aeration in the plates, and temperature and light relations, individually or collectively, may change the morphology of an organism to such an extent that it may be mistaken for a different species.

The size and color of the mycelium and sporophores of a given strain of *Verticillium* may be appreciably altered on different culture media; the number of sets of lateral branches or whorls and secondary branches or whorls which make up the sporophores may be increased or reduced. Similarly the size and number of spores may vary with the substrate, and on some media spore production may scarcely take place at all. Also, continued cultivation on artificial media brings about pronounced morphological changes in the fungus (Chaudhuri, 50; van der Lek, 188; Pethybridge, 149; and author's observations). I have cultures of *Verticillium* which once produced dense masses of black, carbonized hyphae in culture and others which produced sclerotia in such quantity that these bodies formed a continuous, gritty crust on the surface of the medium. With continued cultivation on artificial media these strains have largely lost their ability to produce black mycelium and sclerotia. The colonies now consist of cottony white mycelium with little or no darkening of the medium by black hyphae or sclerotia. In some cultures, spore production largely has been suppressed.

For the reasons just given it is not easy to accept the slight morphological differences existing between the so-called species of *Verticillium* as sufficient claim for specific rank for them. Also, for these reasons, it is not considered worth while at this point to make an exhaustive table of the measurements of the mycelium, sporophores, etc., since by varying the substrate on which these organisms are grown the characteristics of these structures in one species may be altered to conform to the descriptions of those of another. In table 10 the size of the spores and sclerotia of the various species of *Verticillium* and *Acrostalagmus* reported to cause hadromycosis in plants are given. In spite of the fact that the authors of these various species

TABLE 10

COMPARISON OF THE DIMENSIONS OF SPORES AND SCLEROTIA OF VARIOUS SPECIES AND STRAINS OF VERTICILLIUM AND ACROSTALAGMUS PRODUCING HADROMYCOSIS IN PLANTS

Organism	Source	Reported by	Conidia		Sclerotia		Sclerotial cells or Chlamydospores	
			Extreme sizes μ	Average μ	Extreme sizes μ	Average μ	Extreme sizes μ	Average μ
V. albo-atrum	Potato	Reinke and Berthold	5–12 by Circa 3	.....	.....	.....	.....	.....
V. albo-atrum Strain 1717	Okra in culture	Carpenter	5.1–11 by 2.1–3	6.8 by 2.4	21 to 91	34 by 44	7 to 10	8.4 by 8.7
V. albo-atrum Strain 2784	Potato in culture	Carpenter	4.2–9.3 by 1.7–4.2	6.4 by 2.4	31 to 70	45 by 54	5 to 10	8.2 by 8.2
V. albo-atrum Strain 2985	Snapdragon in culture	Carpenter	.....	.....	28 to 70	39 by 57	3 to 15	.....
V. albo-atrum	In culture	Klebahn	4–6 by 1.5–2.5	.....	.....	.....	.....	.....
V. dahliae	Dahlia	Klebahn	4–7 by 1.5–2	.....	.....	50	5 to 6	.....
V. sp.	Apricot in culture	Czarnecki	6.75–11.25 2.25–6.75	.....	50 to 250	.....	.....	.....
V. tracheiphilum	Pepper	Curzi	3.5–5 by 2–3	.....	30 to 50	.....	.....	.....
V. albo-atrum Strain 1685	Eggplant in culture	Carpenter	5.1–8.5 by 2.1–4.2	6.5 by 2.6	31 to 87	51 by 51	.....	7.3 by 9.4
V. angustum	.....	Wollenweber	Spores smaller than V. albo-atrum	.....	.....	.....	.....	.....
V. duboys	Potato	Foëx	5.6–11 by 3–5	.....	25 to 200	.....	5 to 12	7.5
V. ovatum	Red raspberry in culture	Berkeley and Jackson	2 75–6 25 by 1.25–4.25	.....	30 to 60	.....	4 to 10	6
A. caulophagus	Black raspberry in culture	Lawrence	3–7 by 2–3	.....	.....	.....	7 to 12	.....
A. albus	Ginseng in culture	Van Hook	2–5 by 1–2	.....	.....	.....	.....	.....
A. vilmorinii	From China aster	Guéguen	5–7 by 2.5–3	.....	20 to 70	50 to 60	.....	.....

have taken their descriptions of the organisms from widely unrelated cultural sources, some from the diseased plants themselves, others from cultures on artificial media, all of which may have affected the morphology of such structures, there still exists a certain recognizable uniformity in the size of the sclerotia and conidia.

In making a similar table, Carpenter (49) appreciated this point and suggested that the differences between the fungi seemed one of variety rather than of species.

The Relation between Verticillium albo-atrum R. and B. and Verticillium dahliae Kleb.—In 1913 Klebahn (113) isolated *Verticillium dahliae* from dahlia plants and believed it sufficiently distinct from *V. albo-atrum* R. and B. to entitle it to specific rank. Although, as van der Lek (189) has pointed out, the difference between the two organisms in culture is very slight, a number of authors have accepted Klebahn's work. Only a few of these may be said to have given the problem the attention it deserves. Among those who regard *V. dahliae* as a distinct species are van der Meer (191), Dufrenoy (70, 72), Berkeley and Jackson (21), and others.

In his paper Klebahn admits that certain of the morphological and cultural characteristics by which he distinguished between his organism and *Verticillium albo-atrum* R. and B. are of little importance. The great difference between the two organisms is said to be in the abundant production of true sclerotia by *V. dahliae* and the complete absence of such structures in cultures of *V. albo-atrum* R. and B. Whether *V. albo-atrum* produces sclerotia or not depends upon the interpretation of the descriptions and drawings made by Reinke and Berthold (164), authors of that species. It must be admitted that the descriptions and drawings of these sclerotial bodies leave much to be desired, but to me the evidence is quite conclusive that these writers associated true sclerotia production with *V. albo-atrum.*

Reinke and Berthold have drawn a structure which, while somewhat diagrammatic, probably was intended for a sclerotium (see plate 1, fig. 2). It is simply described in the legend as "germinating resting mycelium." Throughout their paper such structures are referred to as sclerotia. Further proof that Reinke and Berthold were familiar with such structures is seen in the fact that they were aware of an error made by Hallier[19] in this connection. If the structures drawn by Reinke and Berthold leave doubt as to their identity, certainly

[19] Hallier, Ernst. Die Plastiden der niedern Pflanzen. Die Kräuselkrankheit der Kartoffeln. p. 7–33. 4 pl. Fue's Verlag (R. Reisland), Leipzig, 1878.

those drawn by Hallier do not. Hallier, studying a fungus which he associated with the disease in potatoes, drew great gnarled masses of thickened carbonized fungal cells which are undoubtedly sclerotia (plate 3). He himself suggested that they looked like sclerotia but concluded them to be the developing fruiting bodies of a *Pleospora*. Reinke and Berthold, reviewing Hallier's work, expressed the belief that, in part, these structures were the "black-brown *Dauermycelium* of *Verticillium*" and not to be confused with *Pleospora* (164, p. 94). Hallier, no doubt, was working with a mixture of several fungi, a fact which Reinke and Berthold also appreciated. In addition to recognizing the sclerotial bodies of *Verticillium* in Hallier's drawings, they thought they recognized the fruiting bodies of another fungus which they referred to the genus *Periola* of Fries. It would seem from this that Reinke and Berthold were perfectly familiar with sclerotia as such.

When Klebahn isolated his fungus from dahlia, he wished to compare it with *Verticillium albo-atrum* R. and B. Accordingly he secured a culture of what was supposed to be that fungus from Dr. Behrens of the Dahlem Biologischen Reichsanstalt. The history of this culture is not given in his paper. He grew the two fungi in parallel culture on various culture media. On these media he observed certain cultural dissimilarities which he himself admitted to be of minor importance. The great difference lay in the ability of the one to produce sclerotia and the inability of the other to do so. The black color which developed in cultures of *V. albo-atrum* was said to be due in part to the presence of much long, black, coarse, little-branched hyphae growing within the medium and in part to the blackened, swollen bases of numerous aerial sporophores which arose from them. The combination of these was said to constitute the sclerotia-like structures which Reinke and Berthold drew. True micro-sclerotia were developed on the other hand only by *V. dahliae*. These could be distinguished at a glance from the blackened mycelium of *V. albo-atrum*.

To me this interpretation of Reinke and Berthold's descriptions and drawings is unacceptable.

Pethybridge (149), working with the disease in potatoes, was the second person to report finding a strain of *Verticillium* which produced only long, carbonized, little-branched hyphae in the medium and not true sclerotia. To what extent he was influenced by Klebahn's work is hard to say, but he also referred to the organism as *V. albo-atrum*.

Van der Meer (191) was the next to take a similar view. She has published pictures which show the difference between the two forms. She, too, regards *Verticillium albo-atrum* as unable to produce sclerotia, in contradistinction to *V. dahliae*, which is said to produce them in abundance (plate 4). In discussing the differences between the two fungi, she remarks that Reinke and Berthold:

> Mention blackened septate hyphae, the short cells of which increase in breadth and become globular, so that the hyphae seems "torulös." When neighboring threads become contiguous, black cell masses are formed of different sizes and of irregular shapes; never, however, are longitudinal partition walls observed. In perfect agreement with this is the accompanying figure of a "Dauermycelium."

She did not add Reinke and Berthold's opinions of these structures, which is as follows:

> All of these brown cells and cellular heaps constitute, as it is easy to show, the resting mycelium for the overwintering of the fungus. This resting mycelium can be called sclerotia even if their cells do not form any larger tissue bodies as is the case in the structures generally designated as sclerotia.

In the following verbatim transcriptions from Reinke and Berthold's paper may be seen the manner in which these writers described the formation of the bodies which they referred to as sclerotia, also the way in which they subsequently used the term at several points in their paper:

> Nachdem die Produktion der Conidien auf der Oberfläche des Stengels eine Zeitlang fortgedauert hat, nimmt das faule Gewebe ziemlich rasch eine intensiv schwarze oder dunkelbraune Färbung an. Die mikroskopische Untersuchung lehrt, dass dieselbe von den sich schwärzenden Mycelfäden des Pilzes herrührt. In denselben treten dabei zahlreiche Querwände auf, worauf die kurzen Zellen stark in die Dicke wachsen und eine kugelförmige Gestalt annehmen, so dass die Fäden torulös erscheinen (vgl. Taf. IX, Fig. 1) [plate 1 in this paper]. Lagern sich mehrere solche Fäden aneinander, so entstehen in dem faulenden Gewebe schwarze Zellhaufen von verschiedener Grösse und unregelmässiger Gestalt. Das Auftreten von Längswänden wurde hierbei nie beobachtet; die braunen Zellhaufen bilden sich also nur durch das Aneinanderlegen benachbarter Zellfäden. Bei der Bräunung verdickt sich die Wand der Zellen merklich, es lassen sich nachher deutlich doppelte Contouren unterscheiden; der Inhalt wird durch die Bräunung grösstentheils verdeckt, meist machen sich jedoch später in ihm ein oder mehrere Öltropfen bemerklich. Die Bräunung erstreckt sich über das ganze im faulenden Stengel befindliche Mycelgeflecht, sogar die unteren Zellen der Conidienträger schwärzen sich später zumeist, und können in ihnen ebenfalls intercalare Theilungen auftreten (vgl. Taf. VIII, Fig. 8) [plate 2 in this paper]. Alle diese gebräunten Zellen und Zellhaufen fungieren, wie leicht zu zeigen ist, als Dauermycelien zur Überwinterung des Pilzes. Man kann diese Dauermycelien Sclerotien nennen, wenn auch ihre Zellen keinen grössern Gewebekörper bilden, wie es bei den gewöhnlich als Sclerotien bezeichneten Bildungen der Fall ist.

Bringt man diese Sclerotien oder Dauermycelien, nachdem sie Monate lang ausgetrocknet waren, bei Zimmertemperatur in Wasser oder in eine feuchte Atmosphäre, so treten aus ihnen farblose Mycelfäden hervor (vgl. Taf. IX Fig. 2, 3) [plate 1 in this paper], aus denen weiterhin bei genügender Zufuhr von Nährstoffen Conidienträger entstehen. (164; page 74–75.)

. . . . . .

Die Conidien sowohl wie die Sclerotien des Pilzes können in der Ackererde vorhanden sein, in welche bei der Aussaat die Kartoffel hineingelegt wird, sie keimen an der Oberfläche der Knollen und der hervorbrechenden Wurzeln und dringen in die letzteren ein. (164; page 91.)

. . . . . .

Die modernden Gewebe derartiger Rückstände einer vorjährigen Kartoffelpflanzung bieten den Conidien wie den Sclerotien von *Vert. atro-album* (sic) den günstigsten Boden für Keimung und Weiterentwicklung. (164; page 92.)

. . . . . .

Zweitens hat man darauf zu sehen, dass die Ackererde, in welche Kartoffeln ausgepflanzt werden sollen möglichst frei sei von Conidien und Sclerotien des *Verticillium*. (164; page 93.)

From the way Reinke and Berthold have used the term 'sclerotia' it would appear that they were familiar with such bodies and associated them with *Verticillium albo-atrum*. While they have used the terms 'sclerotia' and *Dauermycelium* interchangeably, the former is used most and is given preference throughout their paper.

The way in which the sclerotia are formed according to Reinke and Berthold is vague. Today we regard sclerotia-formation as a budding process rather than as an anastamosing of hyphae lying alongside of one another or becoming entwined longitudinally, but Reinke and Berthold believed the black "cell heaps" they saw were formed in this manner.

Certainly the structures drawn by Hallier (see plate 3) were not formed this way and yet, as pointed out earlier, Reinke and Berthold considered them to be sclerotia of *Verticillium albo-atrum*. Reinke and Berthold probably did not devote a great deal of thought or study to the way the sclerotia of *V. albo-atrum* are formed, but there seems to be sufficient evidence that at least they did see them and associate them with their fungus.

Klebahn grew the organism which he isolated from dahlia and the organism which he had secured from Dr. Behrens on salep agar in petri plates at room temperature. At the end of three weeks the diameters of the colonies of both organisms were compared. The fungus obtained from Dr. Behrens and referred to as *Verticillium albo-atrum* grew the fastest. This difference might very easily have

been brought about by conditions under which the experiment was conducted and not taken into consideration by Klebahn.

Van der Meer (191) conducted similar experiments with the two strains of *Verticillium*. Although, like Klebahn, she was seeking to differentiate between the two strains on the basis of differences in the rate of growth, her results seem to be just the opposite to those of Klebahn; *V. dahliae* grew faster than *V. albo-atrum*. She found this true in a number of experiments. Of one of these she says: "After four days the culture of type *A* [*Verticillium albo-atrum*] showed no colonies, or very small ones, just appearing above the agar, those of type *B* [*V. dahliae*] showed well-developed colonies with aerial mycelium."

Confusion like this in the data of various writers makes the claim of *Verticillium dahliae* to specific rank less tenable, if such data is to be considered of importance at all.

Bewley (25) reports having isolated six strains of *Verticillium albo-atrum* from plants suffering hadromycosis, in which the amount of sclerotia in culture varied from an arbitrary standard of 0 per cent (no sclerotia formed) to 100 per cent (total surface of medium covered). Carbonized hyphae were formed in the cultures which produced no sclerotia. From his inoculation studies with these strains he concluded that there was some evidence that virulence is distinctly associated with the amount of sclerotia and carbonized hyphae produced. The number of days for symptoms to appear in inoculated plants dropped from 31 to 12 according to the strain of the organism used, the one with 100 per cent sclerotia producing wilt the quickest of all.

Gravatt (81) is inclined to attribute the erratic behavior of the disease in maples to different strains of the organism, each with a varying amount of virulence.

Haenseler (90) noted that the *Verticillium* which he isolated from peach and which he called *V. albo-atrum* differed from okra and eggplant strains only in the readiness with which it formed sclerotia. The strains from each of these plants differed somewhat from each other in this respect, but he considered them identical, since he found on long cultivation that a single strain of *Verticillium* may show such differences.

It may be asked, if *Verticillium albo-atrum* produces true sclerotia, what was the fungus which Klebahn isolated from dahlia? Also the fungus which he secured from Dr. Behrens to compare with it? In my opinion the fungus isolated by Klebahn from dahlia was *V. albo-atrum*

pure and simple and should be called such. The relation of the strain secured from Dr. Behrens is not so clear, but it was probably the same non-sclerotia-producing form first definitely reported by Pethybridge several years later. Or it may have been *V. albo-atrum* which had been cultivated by Dr. Behrens on artificial media for such a long time that it had lost its ability to produce sclerotia. There is no reason to doubt that Klebahn saw a difference in the two forms, but there is reasonable grounds for doubting whether the fungus he secured from Dr. Behrens for *V. albo-atrum* was true to the type described by Reinke and Berthold.

Klebahn made the differences of sclerotia production between the two forms the great basis of distinction. To me even this distinction is not an important one in view of my experience with the strains in culture. Cultures of *Verticillium albo-atrum* and *V. dahliae* secured from the Centraal-Bureau voor Schimmelcultures at Baarn, Holland, when first cultivated on Czapeck's synthetic nutrient agar, were morphologically quite indistinguishable. Both produced an abundance of microsclerotia. After considerable cultivation on this same medium both forms largely have lost their ability to form these structures. In this respect both forms remain constant culturally.

Foëx (77) also secured cultures of *Verticillium albo-atrum* from the Centraal-Bureau voor Schimmelcultures to compare with *V. duboys*. He mentions that *V. albo-atrum* produced an abundance of spherical or oval sclerotia, 30μ in diameter, which gave a grey and finally a black color to the cultures. It would appear from Foëx's experience and mine that the fungus issued by the Centraal-Bureau voor Schimmelcultures as *Verticillium albo-atrum* R. and B. produces true sclerotia and not merely long, swollen, blackened hyphae.

For the various reasons given above it is suggested here that *Verticillium albo-atrum* R. and B. be considered a true sclerotia-producing fungus, and that form which regularly produces only carbonized hyphae and no sclerotia should be considered merely as a variety of it. Since it commonly occurs on the potato and was first definitely recognized by Pethybridge (149) in diseased potato plants and tubers, it is suggested that it be called *V. albo-atrum* var. *tuberosum*. It is known to attack the cucumber, cherry, and tomato also (van der Meer, 191). The non-sclerotia-bearing form described by Lawrence (117) on black raspberries is probably a very closely related strain of it.

The Relation of Verticillium albo-atrum R. and B. to Other Verticillium Species Known to Produce Hadromycosis in Plants.—As

said elsewhere in this paper (page 207), the several species of *Verticillium* which produce hadromycosis in plants and which have been named since Klebahn described *V. dahliae* in 1913, are seemingly closely related. It would be unwise, however, to attempt to reclassify any of these organisms on the basis of their present descriptions. But these descriptions do tend to indicate that most of these new forms are varieties of *V. albo-atrum* rather than species. At this time a monograph of the genus *Verticillium* based upon morphological, physiological, and genetic studies, as well as cross-inoculation experiments, is sorely needed. Until such a paper appears, any classification must be regarded as tentative.

Dufrenoy (72) regards *Verticillium ovatum* B. and J., which attacks raspberries in Canada, as identical with *V. dahliae* Kleb. This is probably true, but if *V. dahliae* is to be considered merely as a variety of *V. albo-atrum* as suggested above, then *V. ovatum* falls in the same category. Since Berkeley and Jackson (21) were able to distinguish between *V. dahliae* and their fungus by cultural methods it is suggested that *V. ovatum* be called *V. albo-atrum* R. and B. var. *ovatum* B. and J.

In all probability *Verticillium trachciphilum* Curzi and *Acrostalagmus vilmorinii* Guéguen can be handled in the same way, since their differences from *V. albo-atrum* are manifestly very slight. Carpenter (49) supports this view.

Verticillium duboys Foëx, regarded by Foëx (77) and Picado (155) as culturally distinct from *V. albo-atrum,* seems to be very closely related to the latter species, and its chief claim to specific rank lies in its ability to produce a rot in potato tubers. *V. albo-atrum* never has been observed to do this, although at times it may cause a rot of tomato fruits, which it penetrates through the diseased stems, according to Bewley (24, 30). Also Foëx was unable to get his fungus to produce a hadromycosis in potato plants. All of his experiments were conducted on an exceedingly small scale, involving only a very few plants and, as he himself suggests, the matter should not be considered closed until further work has been done to substantiate his results. But if *V. duboys* is unable to attack the plants, then it is outside the limits of this paper and need not be discussed further.

Van Beyma Thoe Kingma (187) renamed the fungus isolated by Foëx from decaying potatoes, *Verticillium foëxii n. s.* although it had already appeared in the literature for five years as *Verticillium duboys* Foëx.

Acrostalagmus caulophagus Lawrence and *A. albus* van Hook are probably more closely related to the non-sclerotia-producing type, called *Verticillium albo-atrum* var. *tuberosum* in this paper.

Verticillium angustum Wollenweber (216) should be discarded. It would be difficult if not impossible to recognize this species from the brief description given of it: It is said to attack the lupine, and its spores were described as "smaller than those of *Verticillium albo-atrum.*" No further description of the fungus has appeared.

CONTROL

Resistant Varieties.—Writers are generally agreed that the ultimate solution of the control problem will probably be found in the development of resistant varieties. Very little or nothing has been done experimentally along this line, however. Resistance as it occurs naturally in the varieties of any given species is discussed under the individual species themselves elsewhere in this paper.

Control with Sprays Not Possible.—It is generally agreed by writers that control of the disease by means of fungicides applied to the tops of the plants is not possible, since infection takes place, almost exclusively, underground in the root system.

Orchard and Field Sanitation.—All writers stress the great necessity of clearing the soil of all infectious material. This means the careful removal of dead and dying plants with as much of the root system as possibly can be lifted, and all plant debris and weeds.

Reinke and Berthold (164) fully appreciated the possible danger of the disease spreading from plant to plant in a row of potatoes when their root systems intermingle. McKay (131) has amply confirmed this view with experiments on potatoes. To effectually block the spread of the disease in the row, he found it necessary to remove not only the plant already showing symptoms of the disease, but also one plant on either side of it, regardless of the healthy appearance of the latter. Shapovalov and Link (176) and Zundel (232) make similar recommendations. Bennett (16) recommends the same treatment for raspberries planted under similar conditions, and van der Lek (190) recommends the same for tomatoes. All diseased material should be burned.

Bewley (25, 28) recommends sterilization of tomato baskets before using them again. He claims the fungus produces a soft rot in the fruit which it enters through the stems.

Pruning.—In California sclerotia may be produced in abundance during the winter on the dead year-old twigs of prune and apricot, and on the fruiting stems of the raspberry killed the preceding spring. They are probably produced on twigs of many other plant suscepts. The killed twigs and stems should be pruned away carefully and burned.

In California an early means of fighting the disease in fruit trees consisted in pruning away all discolored wood. Since in fairly severe cases of the disease such discoloration generally can be traced in an unbroken line to the roots, much cutting was necessary, and in most instances it was impossible to remove all the diseased tissue without destroying the tree. Experience has shown that trees even very severely attacked may exhibit a most extraordinary recovery the year following the attack. It is not unusual to see young apricot trees apparently dead from the disease in mid-summer make a complete recovery; the following year these same trees may not exhibit the slightest trace of disease, and to all appearances are little the worse for their experience.

It is van der Meer's (191) theory that reinfection through the root system must take place afresh each year. If true, this will explain largely the remarkable recovery of very sick trees. Results of preliminary experiments at the Deciduous Fruit Field Station tend to confirm van der Meer's view. In one experiment, apparently healthy, vigorous limbs were cut from prune trees. Throughout the spring and summer these trees had not shown the slightest trace of the disease. The year previous, however, they had suffered a severe attack. The wood laid down the current year was of normal appearance and sharply separated from the second-year wood beneath it, which was discolored. Many cultures were made from the new normal wood and from the discolored wood. *Verticillium* was isolated in many instances from the latter but never from the former. It would seem that the fungus was still alive in the second-year wood but was not able to spread into the new wood.

Gravatt (81) and Colley (51), who quotes Gravatt, working with maples, recommend the careful sterilization of pruning shears in the usual manner with mercuric bichloride, 1/1000, as well as the disinfection and protection of pruning wounds with a paint made of equal parts of coal tar and creosote. No other writers recommend such precautions, and it is somewhat doubtful whether they are necessary in view of the fact that infection takes place almost exclusively in the

root system and not in the tops. It may be that the maple is an exception to the general rule, however.

Dufrenoy (70) recommends the careful removal of the diseased bark tissue on the collar and roots of affected walnut trees and exposing the wounds to sunlight and air. He further recommends cauterizing the wounds with sulfuric acid or iron sulfate.

Weeds.—Since many weeds are susceptible to attack it is essential that those known to harbor the fungus be removed. In California the destruction of pigweed (*Amarantus retroflexus* L.), groundsel (*Senecio vulgaris* L.) and common mallow (*Malva rotundifolia* L.), is advised. Bur clover (*Medicago hispida* Gaertn.), also is susceptible but seemingly less so than the others. Other susceptible weeds are *Urtica urens* L., *Chrysanthemum leucanthemum* L., *Chenopodium album* L., *Erigeron canadensis* L., and *Solanum nigrum* L. (van der Meer, 191, 192); cocklebur (*Xanthium* sp.) and velvet leaf (*Abutilon* sp.) Carpenter, 47; Haenseler, 89; and others).

Crop rotation.—Crop rotation is suggested by most writers as a possible means of eradicating the fungus from contaminated soil. Care must be observed in selecting crops for rotation that an equally susceptible or even more susceptible variety is not used to follow the one which has just been attacked by the disease. Frequently this is done, however, and severe losses have been sustained by growers who failed to observe this precaution.

While the successful cross-inoculation experiments previously discussed clearly indicate what crop sequences should be avoided, certain crop rotations have been specifically advised against:

Sugar and fodder beets should not follow potatoes (Westerdijk, 204; Wollenweber, 216). It is considered inadvisable by Zundel (233) to plant raspberries after potatoes; or after tomatoes and eggplant (Rankin, 163). Berkeley and Jackson (20, 21) and Dodge and Wilcox (61) regard all of these as unsuitable for rotation purposes as does Boyer (35), who adds cucumbers to the list.

Buisman (40) associates the disease in elm seedlings with potatoes.

Raspberries should not follow muskmelons or peaches which have suffered the disease (Bennett, 16), or salsify, okra, or cotton (Dodge and Wilcox, 61).

Black raspberry should not follow potatoes (Zeller, 230) or eggplant and okra (Haenseler, 92).

Eggplant should not follow peppers (Curzi, 54) or udo (Weimer, 203).

Potatoes should not follow cucumbers (Lindfors, 119), or tomatoes (van der Lek, 190), or eggplant (Orton, 136).

Currants should not follow potatoes (van der Meer, 191).

Cherries should not follow potatoes (Anonymous, 4; van der Meer, 191), or cucumbers, tomatoes, or beets (van der Meer, 191).

Apricots should not follow muskmelons or eggplant (Dufrenoy, 72), and should not be planted on land where diseased tomatoes have been growing (author's observations).

Jagger and Stewart (110) made experimental plantings of *Lycopersicum esculentum* Mill., *L. pimpinellifolium* Dunal., *Solanum carolinense* L., *S. rostratum* Dunal., *S. tuberosum* L., *S. marginatum* L., *S. integrifolium* Poir., *S. torvum* (wild eggplant from Porto Rico), *S. eleagnifolium* Cav., and *S. pyracanthum* Jacq. on land previously planted to eggplants which were severely affected with the disease. All were attacked.

Carpenter (49) and Haenseler (89) associate the disease in okra with potatoes. Haenseler associates wilt in okra with peaches, roses, tomatoes, and horse nettle (*Solanum carolinense* L.).

Van der Meer (193) associates the disease in *Ulmus campestris* L., with potatoes.

Berkeley (17) associates the disease in potatoes, eggplant, and raspberry with tomatoes.

Haenseler (94) associates the disease in maples with peach; Oppenheimer (134), with potatoes.

Promoting Vigorous Growth.—Bewley (24, 30) regards rapidly growing succulent plants as more resistant than those grown 'hard,' which is just the reverse of what may be expected to occur in most plants attacked by disease. Checking the growth of plants or starving them in the early stages is said to render them more susceptible.

Temperature and Shade Relations.—Bewley (24, 25, 28, 30) takes advantage of the susceptibility of the fungus to high temperatures. He recommends closing the ventilators in hot houses for several hours a day and increasing the boiler heat to a point unfavorable to the fungus. As soon as the wilt appears the temperature should be raised above 25° C. Since shade also retards the progress of the disease he recommends the application of a thin coating of whitewash to the glass.

Because summer temperatures are generally unfavorable to the disease, certain writers recommend planting susceptible crops as late as possible in the spring (Bewley, 24, 30; Taylor, 185, and others).

See "Temperature Relations" (p. 230), for a further discussion of the relationship between temperature, drought, shade and soil, and the disease.

The Use of Manure.—There is a general agreement that manure, compost, humus, or other organic matter in the soil is favorable to the spread of the fungus (Reinke and Berthold, 164; Pethybridge, 149; Brittlebank, 36; Schoevers, 175; Bewley, 24, 25, 28, 30; Haenseler, 84; Utkin, 186; Blattný, 32; and others). For this reason, the use of such materials as fertilizer should be curtailed as much as possible.

Whetzel and Rosenbaum (206) and Rankin (159) regard the use of a sawdust mulch around ginseng plants with suspicion.

Forcing the Production of New Roots.—Bewley (25, 28, 30), Schoevers (174, 175), and van der Lek (190) recommend the practice of piling clean soil high about the bases of diseased tomato and truck-crop plants to force the production of new roots. Plants so treated may survive until the arrival of summer temperatures which are unfavorable to the development of the disease. With higher temperatures prevailing, the affected plants resist the disease better, and frequently mature and produce a fair crop.

Soil Sterilization.—Many attempts have been made to sterilize the soil with various chemical and physical agents.

Bewley (24, 25, 28, 30) found that if the fungus gains access to soil that has been sterilized its spread is much more rapid than in unsterilized soil.

Steam sterilization is considered practical in the hothouse only where high-priced crops warrant the expense involved.

Pethybridge (150, 151) sought to destroy the fungus in infected tubers without injuring their seed value by heating them. See "Control of *Verticillium* Hadromycosis of Potato Tubers by Heat" (p. 284), for details of this experiment.

Formaldehyde is recommended as a soil disinfectant for use in greenhouses where the production of high-priced crops warrants the expense involved (Schoevers, 174, 175; Whetzel and others, 207). Simpson (178) recommends formaldehyde at the rate of 1 gallon in 20 gallons of water to disinfect the dead tomato stems after harvest.

Preliminary experiments of Blattný (32) indicate that a 2 per cent solution of formalin applied at the rate of 15 liters per square meter is sufficient to disinfect soil in which horse-radish has suffered severely. Schoevers (174, 175) recommends the saturation of the soil in winter with 2.5 per cent solution of formalin. Dufrenoy (70) recommends

commercial formalin, ¼ strength, or concentrated iron sulfate to disinfect the soil.

Blattný (32) claims that a 10 per cent solution of sulfuric acid applied to the soil at the rate of 0.5 liter per square meter will reduce the extent of contamination greatly.

He also states that infection in horse-radish was reduced from 90 per cent to 50 per cent by applications of slaked lime to the soil at the rate of 6 kg per square meter.

Bewley (30) states that *Fusarium* and *Verticillium* infections are reduced in tomatoes when lime is applied to the soil in winter. Haenseler (87, 91, 93) takes just the opposite stand; he contends that acidifying the soil lowers the incidence of wilt while liming increases it:

> Eggplants are more subject to wilt when planted on neutral or alkaline soils than when placed on soils which are quite acid in reaction. For the past four years we have conducted tests to determine whether or not soils acidified with sulfur or green manure would show a reduction in the amount of eggplant wilt. In 1924, the plots which received applications of sulfur in 1922 and 1923 showed appreciable improvement over the plots which had received lime in the two previous years. This year, the differences between the limed and the sulfured blocks are still more marked. Acidifying a soil which is thoroughly infected with the wilt fungus does not seem to control the disease that immediate season but, from the results obtained so far, it seems highly probable that the wilt organism may become less and less abundant or at least less virulent from year to year in a highly acid soil. The sulfured blocks are by no means free from wilt but the disease appears much later on these than on the limed blocks, thus allowing a larger growth and a better crop on the acid blocks.
>
> In 1925, for example, the average height of plants on the plots receiving 1000 lbs. lime, 500 lbs. lime, no treatment, 300 lbs. sulfur, and 600 lbs. sulfur per acre, were 16.85, 17.55, 18.2, 19.05 and 19.65 inches respectively. Aside from this difference in plant height the limed blocks failed to give fruits of marketable size, while a fair crop was obtained on the untreated and the sulfured blocks. The effect of the lime and sulfur is further shown by the difference in the number of plants already showing wilt symptoms this year. On July 6, the blocks receiving 1000 lbs. lime, 500 lbs. lime, no treatment, 300 lbs. sulfur, and 600 lbs. sulfur per acre, were 72.5 85, 55, 22.5 and 7.5 per cent respectively. Furthermore, the plants on the limed blocks are very much smaller than those on the check and sulfured blocks. From these results it would seem advisable, in selecting soil for eggplants, especially in regions where wilt is a serious disease, to avoid fields which are neutral or alkaline in reaction. A field in which the lime requirement is rather high or which gives a pH reaction of 4.5 to 5 is much less likely to give trouble from wilt. It is also evident that applications of lime should be avoided on fields where eggplants are to be placed in the near future (91).

Van Poeteren (196) attempted to sterilize *Verticillium*-infested soil, with unsatisfactory results with cresol and carbolic acid applied

at the rate of 0.5 liter in 20 liters of water to 1 square meter of soil. In certain cases, these chemicals seemed to predispose the plants to even more severe infection.

Ammonium carbonate and copper sulfate give unsatisfactory results with tomatoes, but are said to be very satisfactory in controlling the disease in melons (van Poeteren, 196).

Williams (208) inoculated young tomato plants, 6 to 8 inches in height in pots, with *Verticillium albo-atrum*. The inoculations were made in the stem just below ground level. Fourteen days later, various chemicals were introduced in the pots at the rate of $\frac{1}{32}$ oz., $\frac{1}{16}$ oz., $\frac{1}{8}$ oz. per pot and watered into the soil. Deliquescent substances were applied in water using 100 cc solution per pot. The treatments were repeated three times at weekly intervals. The experiments were carried out in the open, but conditions at the time, presumably climatic, were unfavorable to the development of the disease. Complete wilting did not occur on any plant. The effect of the treatment was determined by counting the number of yellow leaves on the plant which had developed between the treatments. Of the substances tested, several of which had a favorable influence on the course of the disease, he says, "A mixture of magnesium carbonate and lime in equal amounts, potassium permanganate and ferrous sulfate were said to be the most promising." Potassium nitrate and ammonium sulfate apparently exerted their influence through a manurial effect rather than as disinfectants. On the other hand ammonium carbonate and Cheshunt compound appeared to be fungicidal, since their beneficial effect was greatest at the lower concentrations. (The latter was used at the rate of $\frac{1}{2}$ oz., 1 oz., and 2 oz. per gallon.) Calcium chloride was beneficial at low concentrations only.

The above experiment is open to criticism from many angles, all of which need not be mentioned here. Proper methods of determining whether the plants showing yellow leaves were really infected should have been included in the experiments.

Lindfors (119) reports just the opposite results with potassium permanganate; an experiment to disinfect soil with a 0.2 per cent solution was unsuccessful.

Bewley (30) recommends the use of Cheshunt compound, a mixture of 2 parts by weight of ammonium carbonate and 11 parts copper sulfate, at the rate of 1 oz. to 2 gallons of water, as a soil disinfectant only when *Verticillium* infestation in the soil is light. Otherwise steam sterilization is preferable.

Wollenweber (217) has determined the lethal dose of many chemicals applied to the fungus in culture.

Dufrenoy (71) gives a list of chemicals said to be suitable to disinfect the soil. Experimental data obtained with the use of the materials are not given.

INDEX OF PLANTS SUSCEPTIBLE TO VERTICILLIUM HADROMYCOSIS

Verticillium hadromycosis is primarily a disease of dicotyledonous plants. A few exceptions have been reported, but the evidence given in these cases is not wholly convincing.

Table 11 gives a list of those plants reported in the literature as susceptible to attack by *Verticillium albo-atrum* and its related forms. In this list are included several species which have been reported by more than one writer as susceptible to *Verticillium* hadromycosis, which, nevertheless, have probably not been proved susceptible. For instance, several writers have included *Theobroma cacao* L. in their lists of plants susceptible to the disease without evidence of any kind but giving in some cases Guéguen as reference. The disease reported in *T. cacao* L. by Guéguen[20] is not a hadromycosis, and therefore has no place in table 11. *T. cacao* is included there because it is possible that some paper giving authentic evidence of the disease in this plant has been overlooked.

Similarly *Sechium edule, Nicotiana tabacum, Coffea arabica, Manihot utilissima, Musa sapientum, Phaseolus vulgaris* and *Thuja sp.* have been reported susceptible to hadromycosis or to attack by *Verticillium albo-atrum.* More work with the disease in these plants is needed, however, before they can be regarded as susceptible, without reservation.

Lastly a lack of clarity in the reports of a few workers as to just what species of plant they were working with makes it always advisable to consult the text for further information concerning any plant listed in the table. To facilitate this a page reference to the text is given after each species listed in table 11.

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[20] Guéguen, F. Sur une maladie du fruit du cacaoyer produite par une mucédinée et sur la mécan de l'infection. Paris Soc. Biol. 68:221–222. 1910.

TABLE 11

PLANTS REPORTED SUSCEPTIBLE TO ATTACK BY VERTICILLIUM ALBO-ATRUM AND RELATED FORMS

Order	Family	Genus and species
Campanulales	Campanulaceae	Campanula macrantha Fisch.
	Compositae	Aster sp. (p. 319)
		Aster amellus L. (p. 319)
		Aster cordifolius L. (p. 319)
		Aster diffusus Ait. (p. 319)
		Aster ericoides L. (p. 319)
		Aster novae-anglae L. (p. 319)
		Aster novi-belgii L. (p. 319)
		Aster paniculatus Lam. (p. 319)
		Aster tradescantii L. (p. 319)
		Aster vimineus Lam. (p. 319)
		Callistephus chinensis (L.) Nees. (p. 322)
		Chrysanthemum sp. (p. 322)
		Chrysanthemum indicum L. (p. 322)
		Chrysanthemum leucanthemum L. (p. 322)
		Cynara scolymus L. (p. 289)
		Dahlia variabilis Desf. (p. 324)
		Erigeron canadensis L (p. 325)
		Gnaphalium margaritaceum L. (p. 329)
		Senecio cruentus D. C. (p. 323)
		Senecio vulgaris L. (p. 326)
		Taraxacum officinale Weber. (p. 324)
		Tragopogon porrifolius L. (p. 295)
		Xanthium sp. (p. 323)
	Cucurbitaceae	Citrullus vulgaris Schrad. (p. 300)
		Cucumis melo L. (p. 293)
		Cucumis sativus L. (p. 289)
		Cucurbita ovifera L. (?) (p. 292)
		Sechium edule Swartz. (p. 289)
Centrospermae	Amarantaceae	Amarantus retroflexus L. (p. 332)
	Caryophyllaceae	Dianthus sp. (p. 330)
		Lychnis chalcedonica L. (p. 329)
	Chenopodiaceae	Beta vulgaris L. (p. 289)
		Chenopodium album L. (p. 326)
Coniferales	Pinaceae	Thuja sp. (p. 319)
Contortae	Oleaceae	Syringa vulgaris L. (p. 327)
Geraniales	Euphorbiaceae	Manihot utilissima Pohl. (p. 310)
	Simarubaceae	Ailanthus glandulosa Desf. (p. 311)
Juglandales	Juglandaceae	Juglandis sp. (p. 304)
Malvales	Malvaceae	Abutilon theophrasti Medic. (p. 334)
		Gossypium herbaceum L. (p. 306)
		Hibiscus esculentus L. (p. 294)
		Malva alcea L. (p. 325)
		Malva rotundifolia L. (p. 323)
	Sterculiaceae	*Theobroma cacao L. (p. 304)

*This species really has no place in this host table. See text, p. 304.

TABLE 11—*Continued*

Order	Family	Genus and species
Myrtiflorae	Thymelaeaceae	Daphne mezereum L. (p. 325)
Ranales	Berberidaceae	Berberis thunbergii D. C. p. (321)
	Ranunculaceae	Aconitum napellus L. (p. 334)
		Paeonia sp (p. 329)
Rhamnales	Vitaceae	Parthenocissus tricuspidata Planch. var. veitchii Rehd. (p. 321)
Rhoeadales	Cruciferae	Radicula armoracia (L.) Robbins (p. 292)
	Papaveraceae	Eschscholtzia californica Cham. (p. 330)
		Papaver orientale L. (p. 330)
		Papaver rhoeas L. (p. 330)
Rosales	Leguminoseae	Lathyrus odoratus L. (p. 333)
		Lupinus sp. (p. 328)
		Lupinus polyphyllus Lindl. (p. 328)
		Medicago hispida Gaertn. (p. 321)
		Phaseolus vulgaris L. (p. 293)
	Pittosporaceae	Pittosporum tobira Ait. (p. 327)
	Rosaceae	Prunus armeniaca L. (p. 301)
		Prunus avium L. (p. 302)
		Prunus cerasifera Ehrh. (p. 303)
		Prunus cerasus austera Ehrh. (p. 302)
		Prunus cerasus acida Ehrh. (p. 302)
		Prunus communis Fritsch. (p. 300)
		Prunus domestica L. (p. 303)
		Prunus domestica L. var. insititia Bailey. (p. 303)
		Prunus mahaleb L. (p. 302)
		Prunus persica Sieb. & Zucc. (pp. 303, 325)
		Rosa sp. (p. 331)
		Rubus sp. (p. 314)
		Rubus allegheniensis Porter. var. sativus Brainerd. (p. 313)
		Rubus idaeus L. (p. 314)
		Rubus occidentalis L. (p. 314)
		Rubus procumbens Muhl. var. roribaccus Bailey. (p. 313)
		Rubus strigosus Michx. (p. 314)
	Saxifragaceae	Ribes grossularia L. (p. 313)
		Ribes nigrum L. (p. 312)
		Ribes rubrum L. (p. 312)
		Ribes sanguineum Pursh. var. lombartii. (p. 328)
Rubiales	Caprifoliaceae	Sambucus racemosa L. (p. 331)
	Rubiaceae	Coffea arabica L. (p. 305)
Sapindales	Aceraceae	Acer sp. (p. 308)
		Acer negundo L. (p. 308)
		Acer palmatum Thunb. var. rubrum Schwerin (p. 308)
		Acer platanoides L. (p. 308)
		Acer platanoides L. var. schwedleri Koch. (p. 308)
		Acer pseudoplatanus L. (p. 308)
		Acer rubrum L. (p. 308)
		Acer saccharinum L. (p. 308)
		Acer saccharum Marsh. (p. 308)
	Anacardiaceae	Cotinus coggygria Scop. (p. 310)
		Rhus canadensis Marsh. (p. 310)
		Rhus canadensis Marsh. var. trilobata (Nutt.) Gray. (p. 310)
		Rhus glabra L. (p. 310)
		Rhus typhina L. (p. 310)
	Buxaceae	Buxus sempervirens L. (p. 321)

TABLE 11—*Concluded*

Order	Family	Genus and species
Scitamineae	Musaceae	Musa sapiens L. (p. 304)
Tubiflorae	Boraginaceae	Heliotropium sp. (p. 326)
	Labiatae	Mentha sp. (p. 329)
		Monarda didyma L. (p. 329)
	Polemoniaceae	Phlox decussata Hort. (p. 329)
		Phlox drummondii Hort. (p. 329)
	Scrophulariaceae	Antirrhinum sp. (p. 333)
		Antirrhinum majus L. (p. 333)
		Veronica elliptica Forst. (p. 334)
	Solanaceae	Capsicum sp. (p. 294)
		Capsicum annum L. (p. 294)
		Lycopersicum esculentum Mill. (p. 295)
		Lycopersicum pimpinellifolium Dunal. (p. 295)
		Nicotiana tabacum L. (p. 311)
		Physalis alkekengi L. (p. 326)
		Solanum carolinense L. (p. 327)
		Solanum eleagnifolium Cav. (p. 333)
		Solanum floridanum Shuttlew. (p. 334)
		Solanum integrifolium Poir. (p. 332)
		Solanum lycopersicum Trn. (p. 295)
		Solanum marginatum L. (p. 333)
		Solanum melongena L. (p. 290)
		Solanum nigrum L. (p. 321)
		Solanum pyracanthum Jacq. (p. 333)
		Solanum rostratum Dunal. (p. 332)
		Solanum torvum Sw. (p. 334)
		Solanum tuberosum L. (p. 265)
Umbelliflorae	Araliaceae	Aralia cordata Thunb. (p. 300)
		Aralia racemosa L. (p. 319)
		Panax quinquifolius L. (p. 292)
Urticales	Moraceae	Humulus lupulus L. (p. 307)
	Ulmaceae	Ulmus sp. (p. 306)
		Ulmus campestris L. (p. 306)
		Ulmus campestris L. var. latifolia Gillekins. (p. 306)
		Ulmus campestris L. var. monumentalis Ruiz. (p. 306)
		Ulmus campestris L. var. wheatleyi Simon-Louis. (p. 306)
		Ulmus Montana With. (p. 306)
	Urticaceae	Urtica urens L. (p. 329)

FURTHER DISCUSSION OF VERTICILLIUM HADROMYCOSIS IN TRUCK CROPS

Under "Description of *Verticillium* Hadromycosis" (p. 210) only those general symptoms are described which may be expected to occur in any plant affected with *Verticillium* hadromycosis. At this point, and in succeeding sections of the paper, the disease as it affects individual hosts is considered. Symptoms supplementary to those described in the earlier section are given here when such additional symptoms may be expected to occur. The descriptions are based primarily upon observations of the disease in California. If the disease has never been observed in this state upon a variety reported as susceptible by writers elsewhere, the descriptions given are based upon a digest of the literature dealing with the disease in that variety. In such cases the descriptions are accurate only as far as the literature from which they have been drawn is accurate.

By common agreement the work of Reinke and Berthold (164) is the foundation upon which rests all other work done on *Verticillium* hadromycosis. These investigators worked with the disease in potato. For that reason a review of their work and a discussion of the work done by others on this same plant subsequent to it might properly precede the discussion of the disease in other species. All other truck crops are discussed in alphabetical order. The other hosts which follow are gathered arbitrarily into convenient groups, such as "Fruit Trees and Nuts," and "Bush Fruits," and arranged alphabetically within the group.

Irish Potato (*Solanum tuberosum* L.)

Résumé of Reinke and Berthold's Original Work.—In 1879 Reinke and Berthold (164) isolated a species of *Verticillium* which they named *albo-atrum* from diseased potato plants of the variety 'Rothe Amerikaner.' According to them, the disease manifests itself in potatoes in three ways which they designated as forms *A*, *B*, and *C*.

Form *A* appears early in July. The lower leaves of affected plants turn yellow and wither as the disease progresses upward from the bottom of the stalk to the top. Rolling of pinnate leaflets may or may not occur. Brown spots of variable size, and sparse at most, may or may not develop on the leaves. The vascular system is yellowish

and filled with mycelium from the roots to the tops of the plant. At first the mycelium is confined to the tracheae, but on the death of the affected part the fungus easily penetrates the walls of the latter and invades all other tissue including cambium, bast, bark, and even the epidermal hairs. Through the rhizomes the fungus penetrates the tracheae of the tubers to a depth not greater than 15 mm. On cutting away a tuber from its point of attachment to a rhizome the tissue will be seen to be discolored a dark brown due to the presence of blackened fungus threads in the ducts. The fungus overwinters at this point. From infected tubers, the disease form *C* develops when such tubers are planted.

Form *B*, like form *A*, usually appears toward the middle of July. Outwardly the symptoms in the parts above ground are essentially the same in the two forms. Spots of variable size appear on the leaves. These spots enlarge, the petiole bends back, and the leaf withers up. The chief distinctions between forms *A* and *B* are: (1) in form *B* there is a complete absence of mycelium in the ducts of affected plants, and (2) the main stem below ground, and also the larger roots, develop large brown spots and fissures in the bark tissue from which the causal organism can be isolated.

Forms *A* and *B* are said to exist frequently on different stalks of the same plant, and in some instances both forms have been found on the same stalk, which shows a close relationship between them.

The fungus in form *B*, as in *A*, overwinters just within the tuber at the point of its attachment to the rhizome. Just how the fungus manages to reach this position is not made clear by the writers. The tubers produced by plants suffering from forms *A* and *B* of the disease are said to be smaller and fewer in number than those produced on healthy plants.

Like those from form *A*, tubers from form *B* may give rise to plants suffering the *C* form of the disease.

Reinke and Berthold believed at first that form *C* of the disease develops without exception when tubers matured on plants affected with forms *A* or *B* are planted. In form *C* the shoots develop later, grow more slowly, and remain shorter than those from healthy tubers. The leaflets, which never develop the bright green color of healthy plants, do not fully expand but remain stunted and badly curled. The main petiole is bent back. Finally discolored areas appear on both the stems and petioles. These enlarge and the leaves dry up, the lower leaves dying first as the disease progresses upward. The stems below ground, particularly at the base near the seed tuber, develop a

distinct brown discoloration which gradually spreads and involves the entire surface. No mycelium is said to occur in the ducts of the stems above ground, in which characteristic this form of the disease closely resembles form *B*. Further, as in form *B*, the bark tissue below ground may be invaded by the fungus. The seed tubers continue to send up stalks as the older ones die away until their food supply is exhausted, when they rot away naturally. But prior to their disappearance, *Verticillium* never appears in the parenchyma, although it may be found in the cells of the outer cork layer.

Infection of the stalks is said to be accomplished in a most anomalous manner; the fungus localized in the tissue of the seed tuber at its point of former attachment to the rhizome is said to grow out into the cork layer of the epidermis of the tuber and through it and around it, without parasitizing the parenchyma tissue, until the eyes are reached, where it enters the ducts of the developing shoots. As the shoots die away very soon after sprouting, or at least before the plant can complete its growth, no tubers are formed and the disease is thus automatically extinguished in the second generation. While the fungus may spread to some extent throughout the epidermal tissue in autumn when the tubers are kept in damp storage at room temperature, ordinarily the winter is spent in the little spot at the heel end as described. Normally the real invasion of the cork cells of the epidermis is said to occur in the spring after the tubers are planted.

Shoots affected with forms *B* and *C* of the disease are said to look glassy, present an unusual brittleness, and break like glass on being bent. Form *A*, on the other hand, rarely if ever develops this characteristic.

In their final investigations Reinke and Berthold found that tubers from plants suffering the form *A* of the disease occasionally give rise to plants suffering the *B* form of the disease rather than the *C* form. Such plants produce tubers, and through them the disease may be protracted into three generations before it is obliterated.

The vast amount of work done of late years has cleared up many of the anomalies of Reinke and Berthold's work. Those investigators, particularly Pethybridge and McKay, who have devoted much time to the study of the disease in potatoes, do not refer to brown spots on the leaves or to a glassy appearance and brittle consistency of shoots of plants autochthonously infected in the field or infected from diseased tubers planted in healthy ground. It is clear that Reinke and Berthold were working with plants affected with some other disease in association with *Verticillium* hadromycosis and attributed to the latter

certain of the symptoms developed by the other. Spieckermann (181) supports this view.

In 1875 Schenk[21] described a potato disease in which the leaves are brown-spotted and the stems upon which they are borne are glassy and brittle and break readily on being bent. In 1906 and 1911 Appel (5, 9) described this disease again and gave it the name *Bacterienringkrankheit*. It was said to be heritable through the tubers, and neither worker was able to prove it to be due to a parasite of any kind. It may be that Reinke and Berthold confused the symptoms of this disease with those of *Verticillium* hadromycosis.

Symptoms of Verticillium Hadromycosis of the Potato.—The disease picture then, is essentially the same as that already given under "Description of *Verticillium* Hadromycosis" (p. 210), the more salient characteristics of which may be summed up briefly as follows: the affected plants lose their bright green color, and the leaves tend to curl upward along the midrib, thus exposing the lower sides. The lower leaves turn yellow first and dry up very much after the normal manner as the disease slowly progresses up the stem. The internodes become shortened and the plant remains stunted.

Infection may take place at any time during the growing season, but it is the opinion of investigators generally that infection takes place more readily in the cool early spring rather than in hot dry weather of summer. Plants attacked while very young and small may die quickly, displaying all or none of the symptoms described. Plants attacked after maturity, on the other hand, do not show the symptoms of dwarfing to the extent that younger plants show them, if at all. Shortening of the internodes and even rolling of the leaves may be absent. Such plants frequently yield diseased tubers, however.

In the heat of the day, the tips of plants in advanced stages of the disease may droop, but during the night they usually recover their turgidity. As the disease runs its course, the new-formed leaves at the growing tips are smaller than usual and dull looking.

Inside the stems the woody portions are discolored, yellowish at first, and in the final stages of the disease often a pronounced brown. All stems of a plant may not be affected at one time but all are affected before the entire plant dies. Spots or lesions, irregular in size and shape and of a blackish-brown color, may or may not develop on the portions of the main stem below ground and on the larger fibrous roots. These lesions may be very superficial and confined

[21] Schenk, L. Über die Kräuselkrankheit der Kartoffel. Centralbl. Agrikulturchem. 8:280. 1875.

wholly to the epidermis or other portions of the cortex, or they may be deep seated and extend into the woody portions of the stem or root. The fungus may be isolated readily from these lesions or from the discolored woody elements of the plant above and below the ground if cultures are not made too soon after infection has taken place, because the fungus ascends the tracheae rather slowly.

By means of the characteristic discolorations of the vascular system the fungus may be traced through the stolons into the tubers. Ordinarily there is a brown discoloration in the tissue of the tuber immediately beneath the point of stolon attachment. From this point the discoloration may spread out in the vascular system to the distal or far end of the tuber. When transverse sections of such tubers are made, the discolored vascular system is seen as a brown ring lying perhaps one-fourth of an inch beneath the surface. Externally the tubers may appear quite normal, although they are generally smaller and fewer in number than those of healthy plants.

Germination of Diseased Seed.—Symptoms of the disease may appear in the tops well in advance of the appearance of the fungus itself in the tracheae. Pethybridge (149) believes that all shoots produced by diseased tubers are normal at first, and that the fungus does not enter them until growth has well started. In none of his experiments was he able to find mycelium in the shoots until they were well developed and the usual symptoms of leaf-roll, etc., had appeared. At this time the fungus invariably was found just entering the base of the shoots. He attributes Reinke and Berthold's failure to find mycelium in shoots developed from diseased tubers (form *C*) to their failure to appreciate this fact. Dale (60) also noted that shoots developing from diseased tubers were normal at first, later showing the characteristic symptoms of the disease.

Dale also attributes 'blindness' of the tubers (destruction of the eyes) to *Verticillium albo-atrum.* She believes that those eyes not actually destroyed by the fungus in storage develop normally, but that many eyes are killed before the tubers are planted. Pethybridge (149), van der Lek (190), van der Meer (191), and others challenge her views and not without reason; from her report it would appear that in addition to *Verticillium* hadromycosis, some other disease was present in the tubers she had under observation. Tubers diseased by *Verticillium albo-atrum* only, do not develop the warty, corky appearance she refers to in her specimens, and *V. albo-atrum* does not produce a brown external mycelium on the roots and tubers such as she has described. Also, within the plant tissues, the mycelium of *V. albo-*

atrum eventually turns brown and does not remain colorless as she mentions. Lastly, she failed to make inoculation tests. For these reasons her work cannot be accepted without further verification.

Pethybridge (149) does not agree with Reinke and Berthold that the disease is automatically obliterated in the second generation because in his experience:

> No case of the disease has been met with in which the affected plant has failed to bear some new tubers; and since a large proportion of these tubers contain the fungus within them, the disease will spread to the next generation. The disease, therefore, is not extinguished automatically in any given generation of affected plants, as had been supposed.

Permeation of the Tuber by the Fungus.—Hallier,[22] probably working with the disease which we know today as *Verticillium* hadromycosis, suspected the permeation of all parts of the tubers by the fungus, but it was Pethybridge (143, 149) who first conclusively proved this to be true, and at the same time proved falacious the contention of Reinke and Berthold (164), Spieckermann (180, 181), and others, that the fungus is sharply confined to a little region in the tuber just below the point of stolon attachment. With the microscope he was able to trace the fungus from the discolored portion at the proximal (heel) end of the tuber through seemingly healthy, white tissue to the extreme distal (rose) end.

In another experiment, he selected tubers freshly dug in the autumn and proved them to be infected with *Verticillium* in the following manner: He cut away a minute portion of the heel end of each tuber in such a way that it remained hanging to the tuber by a small bit of skin, the two cut surfaces being left exposed. Placed in a moist chamber, if infected with *Verticillium,* the tubers soon developed a growth of aerial mycelium upon their cut surfaces. Any doubt as to its identity was readily dispelled with the microscope. Twenty-five tubers, proved to be infected with *Verticillium* in this manner he cut into halves, heel-end halves and rose-end halves. The following spring a similar lot of potatoes proved to be infected with *Verticillium* in the manner described were cut into halves as before. The four lots of seed thus obtained were planted soon after, and the shoots which developed were examined for the presence of *Verticillium.* The results obtained are given in table 12.

The "misses" in table 10 are accounted for on the basis of predatory attacks of birds, rats, and parasites other than *Verticillium.*

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[22] Hallier, Ernst. Die Plastiden der niederen Pflanzen. Die Kräuselkrankheit der Kartoffeln. p. 7–33. 4 pl. Fue's Verlag (R. Reisland), Leipzig. 1878.

Pethybridge concluded from his experiment and others typical of it that: (1) the fungus is not localized in the heel end of infected tubers even in the autumn when the tubers are dug, because in his experiments a high percentage of diseased plants developed from both rose and heel-ends of potatoes dug and cut in half at that time; (2) that by spring the fungus will have permeated all parts of the tissue of infected tubers to an even greater extent than in the fall, since the percentage of diseased plants obtained from rose-ends of tubers cut away in the spring was considerably greater than that obtained from rose-ends cut away in the fall; (3) that diseased seed tubers may produce sound healthy plants, since a small percentage of plants developed from such tubers never did develop symptoms of any kind and to all appearances were perfectly healthy.

TABLE 12

RESULTS OBTAINED EXPERIMENTALLY BY PETHYBRIDGE TO DETERMINE EXTENT OF PERMEATION OF POTATO TUBERS IN AUTUMN AND SPRING BY VERTICILLIUM

Sets planted		Number of plants developed	Number of misses	Diseased plants with *Verticillium*	Healthy plants without *Verticillium*	Per cent diseased of those developed
Description	Number					
Autumn-cut heels	25	23	2	21	2	91
Autumn-cut roses	25	24	1	15	9	63
Spring-cut heels	25	23	2	22	1	96
Spring-cut roses	25	25	0	19	6	76

McKay (129, 131) has amply verified Pethybridge's work. He reports the following results from one of his tests (129):

The kind of seed pieces used made no essential difference in the amount of infection from *Verticillium albo-atrum* secured either in the plants produced or in the yields obtained, the percentage of infection in the yields from the stem pieces being 22.7 and from the eyepieces 24.6. This difference is entirely negligible, being even less than the difference in the results secured from planting the two longitudinal halves of other tubers which presumably should have shown no difference in amounts of infection in the yields.

From this and several other identical experiments he concludes:

The stem-end seed pieces did not seem to give more disease either in the plants or in the tubers produced therefrom than the eye-end seed pieces of the same infected tubers. The differences are at least so slight that it apparently is not advisable in attempting to avoid wilt in seed potatoes to rely much on the practice of discarding the stem-ends and planting only the eye-ends of tubers suspected of containing wilt organisms.

Edson (73) working along similar lines concluded that: "Stem-end pieces yielded slightly higher percentages of disease than eye-end pieces, evidently because the stem-end is endowed with less physical resistance."

Absence of Color No Infallible Proof of the Health of the Tuber.—Reinke and Berthold (164) and many subsequent investigators contended that the fungus in an affected tuber is strictly localized in a small discolored area only a few millimeters in thickness, just below the point of stolon attachment and that the infected portion can be recognized by the discoloration in the tissue.

Pethybridge (143, 149) discovered, apparently by accident, that this contention is falacious. In one of his experiments he sought to determine just where the fungus is localized in the tuber when it is dug in the fall. He selected tubers from affected plants and cut away a minute portion of the stem-end to determine the presence or absence of color. Those without discoloration he regarded as healthy. Those with discoloration he further divided into two classes: (1) those in which the discolored portion was carefully cut away, and presumably rendered healthy thereby, and (2) diseased. The tubers were planted and observations of the plants which grew from them showed an equal distribution of the disease in all three classes. Thus seemingly sound, healthy tubers with no discoloration at the stem-end were no less free from the disease than those showing discoloration or those from which the discolored portion had been so carefully removed. A weak point of this experiment may be found in the fact that the seed was planted under ordinary field conditions, and the plants may have become autochthonously infected in the soil.

Edson (73) and McKay (129, 132), studying *Verticillium* and *Fusarium* hadromycosis of potato tubers on a vast scale, conclude from their investigations that the absence of discoloration from tubers cannot be considered evidence of their sterility.

In one experiment with tubers from plants known to have been affected with *Verticillium* hadromycosis, McKay (129) found by cultural means that as many as 14.4 per cent of the tubers were infected but showed no discoloration. In a group of similar experiments covering a period of four years and involving the making of cultures from over 12,000 tubers, he found that the number of infected tubers which showed no discoloration averaged 6.6 per cent.

Presence of Color No Infallible Proof of Disease in the Tuber.—Whereas formerly much stress was placed upon the discoloration in tubers as a means of detecting parasitic diseases, today investigators

are generally agreed that the presence of discoloration is by no means an infallible indication of the presence of parasitic organisms. Edson (73) concludes "that a superficial necrosis may develop in the stem tissue of apparently normal stock," and Heald (102) states that varieties with stolons which extend into a deep depression at the stem-end may show a discoloration at the point of stolon attachment that is natural. Barrus and Chupp (14) attribute stem-end discoloration to chilling and to unknown causes while Edson (73) secured deep discoloration which he believes "to be the direct result of too rapid respiration induced in the soil at high temperatures such as prevail during the summer months" in certain localities. Numerous forms of discoloration may be induced by improper storage conditions, and in the field, shortage of water, lack of proper nutrient materials, improper growing conditions, etc., all tend to bring about internal discoloration of the tubers of characteristic type and to which characteristic names have been given. No further discussion of such troubles need be given here.

Since the discoloration ordinarily produced at the stem-end of tubers infected with *Verticillium* may be confused very easily with discoloration which is wholly natural or of physiological origin, the only sure way of proving the presence of this parasite is by cultural methods.

Relation of Verticillium Hadromycosis to Stem-End Discoloration of Tubers.—While many investigators have come to realize that the presence or absence of color in the tuber is no trustworthy index to its health, McKay (129, 131) and Edson (73) have done more than any other investigators to determine the relationship between tuber symptoms and the occurrence of organisms therein. McKay's work is the most pertinent since his studies were more closely concerned with *Verticillium*-infected tubers. He reports the following experiment (129):

> Six hundred Up-to-Date tubers grown in 1917 in hills attacked by *Verticillium albo-atrum* were cultured by the method outlined above. Nearly three-fourths of them (439 tubers, or 73.2 per cent) yielded *V. albo-atrum* in culture. Of these, 70.8 per cent were 'browned' in the vascular region at the stem-end, 19.6 per cent were 'yellowed' and 9.6 per cent were 'not discolored' at all. Of the 95 tubers in this lot which gave no organism in culture, 18.9 per cent were 'browned' in the vascular region, 17.9 per cent were 'yellowed,' and 63.2 per cent were 'not discolored.' There were 111 tubers altogether which had no discoloration in the vascular region. Of these 54 per cent gave no organism in the cultures; 8.1 per cent gave 'miscellaneous fungi', to which no importance can be attached, for they probably cause no disease in potatoes; while more than a third, 37.9 per cent, gave *V. albo-atrum*. Of all the tubers which were 'browned,' 14.2 per cent gave

no organism of importance, and 84.3 per cent gave *V. albo-atrum.* Thus, if this lot of tubers had been sorted for seed on the basis of the presence or absence of discoloration in the stem-end vascular region, 38 per cent of those passed as fit for seed would have been infected with *V. albo-atrum,* while 14 per cent of those eliminated for seed purposes would apparently have been entirely free from a wilt-producing organism.

. . . . . .

In another lot of 647 tubers of seven varieties grown in 1917 from disease-free seed potatoes on soil badly infested with *Verticillium albo-atrum,* nearly half of them, or 293 tubers, were 'browned' in the vascular region. These when cultured gave 55.3 per cent *V. albo-atrum.* . . . .

. . . . . .

In another lot of 498 potato tubers of seven varieties grown in 1917, from disease-free seed potatoes inoculated at planting time with pure cultures of *Verticillium albo-atrum,* 232 tubers were 'browned' in the vascular region. These when cultured gave 60.5 per cent *V. albo-atrum,* 9.6 per cent *Fusarium radicicola,* 26.5 per cent miscellaneous fungi, and 2.1 per cent no organism. Of 244 tubers which gave *V. albo-atrum* in cultures, 0.8 per cent were affected by 'jelly end' or slight dry stem-end rots, 2.9 per cent were 'blackened' in the vascular region, 82.4 per cent were 'browned,' 13.5 per cent were 'yellowed,' and only 0.4 per cent were 'not discolored.'

. . . . . .

In still another lot of 258 Up-to-Date potato tubers grown by plants wilted naturally in the field with *Verticillium albo-atrum* during the season of 1916, 75 were 'browned' in the vascular region. These when cultured gave 57.3 per cent *V. albo-atrum.* . . . .

Summing up his experiments over a period of three years, involving the study of 12,136 tubers, 2,097 of which yielded cultures of *Verticillium* he found that:

Only a small percentage, 1.1, were 'blackened' in the vascular region. The great majority of the tubers, 64.6 per cent, were 'browned'; a large portion, 26.2 per cent, were 'yellowed' while a comparatively small though appreciable number, 6.6 per cent, were 'not discolored.'

He concluded from the experiments:

that this fungus when present in potato tubers is accompanied in the majority of cases by distinct discoloration but that frequently the discoloration is very light or even entirely absent and that therefore discoloration of the tubers is not a reliable basis for judging whether or not this fungus is present.

Edson (73), working both with *Fusarium* and *Verticillium*-infected tubers, concludes:

In the material studied, vascular discoloration of stem-end tissues of Irish potato tubers was not found to be proof of the presence of parasitic fungi. Discolored bundles were often sterile, and fungi were frequently isolated from tissues which appeared normal.

Intensity of Discoloration in Tubers and Stems as a Basis of Differentiation between Hadromycosis Due to Verticillium and to Fusarium.—The symptoms of *Verticillium* and *Fusarium* hadromycosis are so nearly identical in many plants, including the potato, that cultural methods must be resorted to, to distinguish between them. Numerous workers, however, have sought to differentiate between the disease on the basis of a possible difference in the intensity of discoloration in the woody elements of plants affected with the two diseases.

Thus Orton (137), Heald (102), Bailey (12), and Barrus and Chupp (14) regard the discoloration in tubers affected with *Verticillium* hadromycosis as darker than that in tubers suffering from *Fusarium* hadromycosis. McKay (129), on the other hand, says that the discoloration in tubers infected with either *Fusarium radicicola* or *F. oxysporium* is darker than that produced by *Verticillium.* In a later paper McKay (131) says the discolorations produced by *Verticillium* and by *Fusarium* cannot be used to distinguish reliably between the two diseases.

Any method of differentiating between the two diseases on the basis of discoloration in the tubers is probably untrustworthy. The abundant work of Pethybridge (149), McKay (129, 131), and Edson (73) clearly shows that the presence of discoloration in tubers is no index to their health, and the absence of it, no proof that they are not infected.

All shades of discolorations from a brown-black to a faint yellow may be encountered in tubers infected with *Verticillium,* the lighter browns preponderating. Because of this constant variation in color and because *Fusarium,* and even nonparasitic diseases, may produce similar discolorations, no attempt to differentiate between the two diseases on the basis of color alone in tubers and stems should be taken seriously.

Heald (102), Barrus and Chupp (14), Orton (137), and McCubbin and others (127), working with potatoes, and Bewley (28) working with tomatoes, believe that the mycelium of *Fusarium* rarely ascends higher in the stems than perhaps a foot above ground, whereas *Verticillium* is known to ascend to the highest tips of the stems and even into the petioles and veins of the topmost leaves.

It should be recalled that *Verticillium* ascends the vessels very slowly and may produce symptoms in the tops well in advance of its actual invasion of those parts, consequently any attempt to differentiate between the two diseases on the basis of mere presence or absence of mycelium in the vessels of the upper portions of the plant should

not be relied upon, especially in the early stage of the disease. The difference in color of the mycelium and its morphology may serve as a possible basis of differentiation, however. Cultures should be made for absolute proof.

At times under certain conditions in California, the stems of potatoes, particularly at or below ground level, as well as the tap and fibrous roots, may show an even brown discoloration of the woody elements which seems to be wholly normal. No organisms can be isolated from such plants, and the tops, if not suffering for lack of water, present a healthy appearance. This discoloration in the wood may be very misleading at times, however, and may be mistaken for that of *Verticillium* or *Fusarium* hadromycosis, especially when accompanied by symptoms of wilt in the tops occasioned by insufficient moisture in the soil. The absence of dead leaves at the base of such plants is a partial help in differentiating these symptoms from those of *Verticillium* or *Fusarium* hadromycosis.

Verticillium hadromycosis formerly was, and still may easily be confused with 'leaf-roll' (*Blattrollkrankheit*) which at times it greatly resembles outwardly. The absence of discoloration in the main stem of plants affected with 'leaf-roll,' and particularly the absence of the fungus from the ducts, permit of an easy differentiation between the two diseases. There are many other differences between them, but it is unnecessary to discuss them here.

Relation of the Size of Tubers to the Extent of Infection.—Reinke and Berthold (164) realized that all the tubers on a diseased plant do not necessarily become infected. They reported that only one-fifth or one-sixth of a large number of tubers from sick plants examined by them revealed the fungus in the ducts at the point of stolon attachment.

Pethybridge (149), on the other hand, studying the location of mycelium in tubers from sick plants states that "Very few of the tubers produced by such plants are free from it." He further adds:

> All tubers borne by an infected plant, however, do not necessarily become infected. As a rule the fungus only reaches the older and larger tubers while the smaller and younger ones often remain free from invasion. Here it may be stated that the tubers which do not become infected with the mycelium of the fungus produce, when planted, absolutely healthy plants and their progeny continues to do likewise.

Curzi (56) supports this view.

McKay (129) says:

> There is no theoretical reason for supposing that there would be any correlation between size and percentage of infection except that tubers from diseased plants

are likely to be smaller than those from healthy plants, although late-formed tubers which would tend to be small in size would also be likely to show less infection than older ones because exposed to danger of invasion by the fungus for a briefer period. This would perhaps be counterbalanced by the presence of a larger amount of infective material in a field at the close of the season than at the start due to the general progress of the disease.

He does not verify Pethybridge's observations relative to the relation between size of tubers and the extent of infection. From his data obtained from 12,136 tubers from nine varieties and produced under a wide variety of conditions over a period of three seasons, he concludes that:

Verticillium albo-atrum was present to a smaller extent in the medium-sized tubers than in those of small or of large size, there being a steady decrease in percentage of this organism from 25.5 in the tubers weighing ½ ounce down to 9 in those weighing 7 ounces, then an increase up to 16.4 per cent in the 11-ounce tubers.

He concludes from his data:

(1) That the smaller potatoes should not be used for seed purposes, because they are apt to contain a higher percentage of wilt infection than the medium-sized tubers unless it is known that the plants by which they were grown were free from wilt, in which case, of course, the small potatoes could be used with safety, and (2) that wilt can not be avoided merely by the selection from the bin of only the medium-sized or even the larger healthy-looking potatoes, as even these may contain a high percentage of wilt infection.

Relation of the Shape of Tubers to the Extent of Infection.—Opinions may vary as to the relation of the size of tubers to the extent of infection in them, but all writers with but one exception, seem to agree that there is no relation between the shape of tubers and infection. Barrus and Chupp (14), however, describing *Fusarium* and *Verticillium* hadromycosis of tubers collectively, report: "Tubers that become diseased early in their development may exhibit a knob or nipple at the stem-end instead of the normal depression at the point of attachment."

Under California conditions no such swelling or protuberance as is described by these writers has been observed nor do any of the other writers who have described the disease elsewhere report such a phenomenon in connection with *Verticillium* hadromycosis. McKay, who has worked with the disease in Oregon for a number of years, during which time he has closely studied many thousands of *Verticillium*-infected tubers, has seen no relation between such protuberances on the tubers and the disease.[23]

[23] Personal letter.

Relation Between Infected Tubers, Diseased Plants, and Yields.—Numerous investigators have appreciated the fact that infected seed does not necessarily always produce diseased plants; also, that the extent of infection in the tubers from sick plants derived from diseased seed varies considerably.

The explanation of these phenomena by Pethybridge (149) is noteworthy:

It is quite conceivable—although it has not been definitely proved—that the strongly infected tubers give rise to plants which show the disease early and soon die off, and that the less strongly infected ones produce plants which attain more normal size, and which do not show symptoms of the disease until considerably later. Finally, the fact that affected tubers occasionally produce healthy plants may be explained by the original infection of the tuber being so slight that the fungus was unable to reach the plant developing from such a tuber before the conclusion of its growth.

Utkin (186) supports this view.

Having satisfied himself from his observations that all shoots from diseased seed are healthy at first, Pethybridge (149) further concludes:

There is, however, a distinct pause of longer or shorter duration before the mycelium proceeds from the tuber to the stalk, during which temporarily healthy stalks are developed from affected tubers. If this pause is sufficiently prolonged, either because the amount of mycelium in the tuber was originally very small, or its location was removed so far from the developing shoot that the latter could not be reached in time, then it is possible to understand how an affected tuber may give rise to a plant which remains healthy throughout the season and which produces healthy progeny.

Statistics, compiled for the seasons 1912–1925, show that when affected tubers are planted 96 per cent of them give rise to diseased plants bearing further affected progeny while the remaining 4 per cent produce healthy plants with healthy progeny.

Verhoeven (200) planted the tubers harvested from 98 diseased plants. Thirty per cent of the progeny was diseased. In this instance apparently no attempt was made to determine what percentage of the tubers used for seed were actually diseased. Since diseased plants may produce some healthy seed, it is possible that some of the seed in this experiment was healthy, which explains the difference between Verhoeven's figures and those obtained by Pethybridge, who knew that all the seed he planted was infected.

McKay (129) has sought to determine the extent of the infection in the yield from plants grown from diseased seed. Referring to his experiment he states:

Plants grown from seed potatoes from which *Verticillium albo-atrum* was isolated before planting frequently developed wilt and gave 29.7 per cent of *Verticil-*

lium infection in the yields. However, not all of the plants grown from the known *Verticillium*-infected seed were affected by the wilt disease, consequently the percentage of diseased tubers in the yields was considerably lower than it would have been if all the plants had wilted. It was high enough, however, to indicate that infected seed is a very serious factor in carrying the disease from one year to the next. The tubers produced by one lot of rather badly wilted plants showed 40.2 per cent infection with *V. albo-atrum* when cultured, and another lot gave a crop containing 49 per cent infection. The highest percentage of *Verticillium* infection found in the tubers produced by any considerable number of plants was 92. This result was secured in the yield of 28 plants of the variety Up-to-Date, which is very susceptible to this wilt. In a number of instances individual plants of several different varieties have given yields with 100 per cent *Verticillium* infection. The average, however, as shown by the records, is nearer 30 to 50 per cent. Some of the plants grown on clean soil from tubers from which either other organisms than *V. albo-atrum* or no organisms were isolated before planting also gave a rather large percentage of *Verticillium* infection in the yields. For instance, the seed potatoes from which only 'miscellaneous fungi' were isolated gave 13.3 per cent *Verticillium* infection in the yields, and those from which no organisms were isolated gave 18.9 per cent *Verticillium* infection. This high wilt infection in these two lots apparently came from the spread of the *Verticillium* fungus from neighboring diseased plants in the field during the growing season, as will be shown more in detail in a later paper.

Writers are generally agreed that plants may be infected so late in the season either from the seed piece or autochthonously from the soil that the tops may show little or no sign of the disease. Such plants may produce infected tubers, however, according to McKay (132).

Relation of Infection to Keeping Quality of the Tubers.—Virtually all writers are agreed that *Verticillium albo-atrum* never causes the decay of tubers in the soil. Similarly, infected tubers are generally believed to keep as well as healthy tubers under satisfactory storage conditions.

Reinke and Berthold (164) report the inability of the fungus to penetrate healthy tuber parenchyma tissue because of the production of a cork layer beneath the point of infection. Pethybridge (149) has verified this.

Barrus and Chupp (14) regard infected tubers as being firmer than those of healthy plants.

An occasional reference is made to the decay of tubers by *Verticillium:* Marchal (122) reports finding a *Verticillium,* morphologically identical with *V. albo-atrum* but biologically different in that it rots the tubers. Similarly, Foëx (77) reports the rotting of tubers by a *Verticillium* which he regards as biologically distinct from *V. albo-atrum* and which he has tentatively given the name *V. duboys* pending further studies.

Rotting of tubers by *Verticillium* must be considered decidedly the exception rather than the rule. No such decay has been reported by American writers with the exception of Carpenter (48). He secured a rot of tubers with *Verticillium*, but, as he himself and Pethybridge (149) point out, his experiments are open to criticism, and the results are doubtful because of the way the experiments were conducted.

McKay (129) has shown that tubers may be infected by more than one organism. He reports no decay or difference in the symtomology of such tubers. *Fusarium* was occasionally found in association with *Verticillium*, and in at least one instance he isolated three miscellaneous fungi from a tuber infected with *V. albo-atrum*.

Susceptibility of Potato Varieties to Verticillium Hadromycosis.— Considerable difference of opinion exists as to the susceptibility or resistance of various potato varieties to the disease.

Van der Lek (190) is emphatic in his recognition of a variation in the resistance and susceptibility of different varieties, although he does not mention these varieties by name. In attempting to explain this variation he states:

> Also, inside factors in connection with the structure of the plant no doubt are of influence. This is seen, for example, in the fact that one potato strain is more susceptible to verticilliosis than another. It is difficult to explain this, especially with a disease of this kind in which the fungus works almost entirely in the wood vessels during the first stage. It looks to me as though the greater or less susceptibility is determined in the first place by the physiological properties of the living protoplasm of the smallest rootlets.

Pethybridge (149), working with the Up-to-Date, Shamrock, and Northern Invincible varieties concluded the Shamrock to be the most resistant of the three. His conclusions would bear more weight had he used more than one plant of each variety in his inoculation experiments.

Utkin (186) concludes that there is considerable variation in varietal resistance and susceptibility to the disease, and he associates this with the varying susceptibility of the varieties to attack by root-destroying insects and microorganisms, since he believes that *Verticillium* can enter the plant only through wounds. Such an explanation is unsatisfactory because it has been sufficiently demonstrated that the fungus can attack healthy uninjured roots readily.

Spieckermann (181) believes there is considerable variation in varietal resistance, pointing out that the Magnum Bonum and Up-to-Date varieties are very susceptible. He believes all red varieties to be more susceptible to the disease, but advances no experimental data to sustain this contention.

Wollenweber (216) believes the following varieties show a definite resistance to *Verticillium*: Erste von Frömsdorf, Elter von Wohltmann, Bismark, and Primel. These show the greatest resistance, while Wohltmann and similar varieties, also Professor Gerlach, Aguste Viktoria, and Lotos, are fairly resistant. Others showing a certain resistance are Jubel, Odenwälder Blaue, Heimat, Bojar, and Topas.

McKay (131), on the other hand, working with twelve varieties over a period of several years, sees no material variation in the susceptibility of varieties to the disease and he says:

> Comparative tests with some of these and observations on the others have indicated no significant difference in susceptibility to the disease. Some varieties give a lower percentage of infected tubers in wilted hills than others, but this appears to be due to earliness of maturity rather than to resistance to the disease. It is sufficient to say that at the present time no use can be made of this factor in the control of the disease.

The paper from which this quotation was taken was published 5 years later than the one quoted on page 279, in which he refers to the Up-to-Date variety as being very susceptible to the disease. McKay's ideas with regard to susceptibility of potato varieties may have changed in the meantime, or it may be that he never intended the Up-to-Date variety to be considered as more susceptible than any other, although that is the idea conveyed in the earlier paper.

Barrus and Chupp (14) regard all varieties as about equally susceptible.

The following varieties have been reported susceptible to attack by *Verticillium*. The numbers in parentheses following the name of the variety or varieties refer to the numbers of the publications in the bibliography at the conclusion of this paper in which the variety is reported susceptible. Rothe Amerikaner, Sebec (164); Early Rose (131, 132, 164); Garnet Chili, Gold Coin, Netted Gem, Earliest-of-All, Pride of Multnomah, Burbank, Rural New Yorker, American Wonder, Uncle Sam (131, 132); Producer, Sir Walter Raleigh (129); Irish Cobbler (129, 131, 132); Up-to-Date (Pacific White Rose) (129, 131, 132, 137, 149); Magnum Bonum (181, 212); Epicure (24); Cumming's Pride (128); Factor (137); Black Skerry, Leinster Wonder (143); Duchess of Cornwall (144, 149); Northern Invincible, Shamrock, Beauty of Hebron (149); Schotsche Muis, Kerr's Pink, Bintje, Ehnola, Abundance, Geeltjes, Blauwpitten, Fontein, Lembke's Industrie, Excelsior, Koksiaan, Andijker Muizen, Schoolmeester, Deodora, Triumph, Lena, Malta, Lieuwe, Parnassia, Paul Kruger, Blauwe, Zeeuwsche Blauwe, Roode Star, Bravo, Thorbecke (191, 192);

Eigenheimer (191, 192, 200); Spaulding Rose (288, 293); Erste von Frömsdorf, Elter von Wohltmann, Bismark, Primel, Gerlach, Aguste Viktoria, Lotos, Jubel, Odenwälder Blaue, Heimat, Bojar and Topas (216); King Edward, Ally (153).

Method of Attack by the Fungus in the Soil.—With few exceptions it is the general consensus of opinion that regardless of the host, plants are attacked under the ground through their root systems. The potato and dahlia alone seem to offer an additional seat of attack, namely, through infected tubers.

Reinke and Berthold (164) showed that infected tubers may produce diseased plants, but erroneously concluded that the fungus reaches the new stalks only by way of the skin. Only in the last stage of decomposition of the seed piece in the soil did they recognize the possibility that the fungus might reach the stalks by way of the tuber parenchyma which it might attack as a saprophyte. Primary infection of plants from healthy seed they regarded as taking place exclusively through the healthy roots.

Pethybridge (149) and MacKay (131, 132) have verified this last point. Neither was able to induce an attack through healthy seed pieces planted in the soil. For this reason McKay considers it useless to plant whole potatoes as seed to avoid the disease, which is known to be effective in preventing an attack by *Fusarium*. *Fusarium* will readily attack and rot healthy seed pieces, making its attack in the exposed parenchyma and gaining entrance to the shoots through it. *Verticillium*, on the other hand, is unable to do this and makes its attack wholly through the roots.

Losses Due to Verticillium Hadromycosis of Potatoes.—While all writers are generally agreed that the losses occasioned by the disease are appreciable, few have attempted to evaluate them because of the difficulty of doing so. The disease is an insidious one, generally running its course over a protracted period of time. The losses occasioned by it vary greatly with the time and extent of infection in the plant. Tubers from plants affected early in the season are generally smaller, fewer in number, and inferior in quality, according to the extent of discoloration in them, etc. The crop from plants affected late in the season may be normal to all appearances in quantity and quality. Such tubers, however, are frequently infected with the fungus and their value for seed purposes destroyed. Pethybridge (149) and Spieckermann (181) support this view.

Pethybridge (149) studying losses occasioned by the disease in Ireland reports as follows:

As regards losses, these are not easy to estimate, but for the whole country they cannot at present be considered serious. Weighings were made in 1914 of the yields of diseased and healthy plants growing under similar conditions of cultivation on one and the same type of soil. The average yield per plant of forty-seven healthy plants was 36 ounces, while that of forty-two diseased plants was only 27 ounces, so that there was a loss of one-quarter of the crop owing to the disease. The plants were growing in both cases in very poor soil, and in the absence of the usual dressing of farm-yard manure, and it is quite possible that in a rich and well-manured soil the difference in the yields between healthy and diseased plants might be still more pronounced. Hence if the disease by any means became widespread throughout the country, the losses might be very considerable.

McKay (129) sums up the losses occasioned the State of Oregon as follows:

It causes appreciable losses each year, not only in commercial fields but especially in seed plots, because the presence of this fungus greatly lessens the value of the potatoes for seed purposes. It annually is responsible for the failure of a considerable number of fields to pass inspection for certification. The yields of affected plants are reduced on the average of from 30 to 50 per cent.

McCurry (128) reports the following experiment and the losses determined from it:

Two small plots were planted with the same number of sets of uniform size of the variety of Cumming's Pride. The seed used in one plot was from healthy plants while that from the other was cut from tubers which showed deep stem-end browning and were the progeny of wilted plants. The plot in which the healthy seed was used yielded 48 pounds, while the yield of the diseased plat was 33 pounds. This would be a reduction of about 60 bushels per acre in a field of 100 per cent diseased stock.

Utkin (186) reports losses as high as 25 per cent in the vicinity of Moscow, Russia.

The losses occasioned by the disease in California are unknown, but they are undoubtedly greater than is generally supposed. The fungus is wide-spread both in the interior and coast counties. There can be little doubt that much of the wilt observed in the coast districts which is now attributed to *Fusarium* is due to *Verticillium*. The disease is little known to the growers at large, and many mistake the symptoms, such as wilting and stunting of the tops, for those of inadequate water supply and poor soil, particularly when much of the field is infected as is frequently the case.

Species of Verticillium Reported Producing Disease Symptoms in the Potato.—Since Reinke and Berthold (164) isolated *Verticillium albo-atrum* from potatoes, a number of species of the fungus have been described and reported to produce typical hadromycosis in other plants. At least three of these are reported on the potato.

Van der Meer (191) considers *Verticillium dahliae* Kleb. as a distinct species and has experimentally proved it capable of producing a hadromycosis in potatoes identical with that produced by *V. albo-atrum.*

Foëx (77) has described a fungus which is said to attack potato tubers through the stolons much after the manner of *Verticillium albo-atrum,* but which differs from the latter chiefly in its ability to produce a rot in the tubers at the point of stolon attachment. In very limited experiments he was unable to produce a hadromycosis in the tops. He hesitated to call this organism by a specific name but has referred to it as *Verticillium duboys* pending further studies. Picado (155) reports this fungus physiologically distinct from *V. albo-atrum.*

Marchal (122) also reports a *Verticillium* which rots potato tubers.

Berkeley and Jackson (20, 21) have given the name *Verticillium ovatum* to a fungus which is said to produce hadromycosis in red raspberries. This fungus also attacks the potato.

Pethybridge (149, 152) reports finding two distinct species of *Verticillium* which are incapable of producing disease of any kind in potatoes but which live saprophytically on the skin of tubers suffering from other diseases. He has named them *V. nubilum* and *V. nigrescens. V. nubilum* was found on the surface of a tuber attacked by *Phytophthora infestans,* and *V. nigrescens* was found on the skin of a potato with ordinary 'scab.' Neither fungus was able to invade tubers or stalks of the potato in his experiments.

For a further discussion of the several putative species of *Verticillium* referred to above see "Discussion of Verticillium Species Associated with Hadromycosis" (p. 244).

Control of Verticillium Hadromycosis of Potato Tubers by Heat.— Pethybridge (150, 151) conducted experiments to control the disease in infected tubers with heat as follows:

He selected twenty tubers and proved them to be infected by cultural methods. These were then segregated into four lots of five tubers each. The first lot received no treatment. The remaining fifteen tubers were placed in an incubator at 46° C with a thermometer stuck, bulb end, into one of the tubers. The temperature recorded was 15° C at the start and it rose 6° within three-quarters of an hour. After two and one-half hours it had risen to 39° C and at the end of five hours it was 43° C at the center of the tuber. At this stage five of the tubers were removed from the incubator and allowed to cool at room temperature. Five hours later an additional five tubers were removed and the last five were removed twenty hours after the start

of the experiment. The temperature within the tubers heated ten and twenty hours was 44.5° C in both instances at the time of removal.

Eventually the tubers were planted, each one in virgin loam in a pot by itself and placed in a cool greenhouse. All twenty tubers had already sprouted at the time of planting, showing that none had been killed by the heat, although the tubers heated for twenty hours had become considerably shrunken. The plants produced by these five tubers incidentally were somewhat smaller than any of the others.

All of the controls (unheated) developed the disease, and those from tubers heated for five hours were even more severely attacked than the controls. The plants from tubers heated ten hours were, for a considerable period, the best looking and those heated twenty hours the next best.

At the conclusion of the experiment, all the plants from control tubers and from those heated for five hours had succumbed to the disease, as did three of the lot from tubers heated for ten hours. One tuber of this lot produced plants of doubtful health, and the remaining tuber produced a healthy plant. Of the lot heated for twenty hours, all plants were healthy and quite free from the disease.

He repeated his experiment the following year, primarily to study the effect of the treatment on the plants derived from heated tubers (151). On this occasion he observed no adverse effects whatever in the tops, and the yield from such plants was normal.

It would appear from his work that the fungus may be destroyed effectively within the tuber by heating for twenty hours at 44.5° C without impairing the vitality of the plants derived from it in any way.

Edson and Shapovalov (75), studying the heat relations of *Verticillium albo-atrum* in culture, were struck by the susceptibility of the fungus to heat and recognized the possibility of controlling the fungus in tubers by heating them.

Bibliography.[24] Anonymous (3, 46); Appel (**5, 6,** 7); Appel and Schlumberger (8); Appel and Wollenweber (9); Averna-Saccá (10, **11**); Bailey (12); Barrus and Chupp (14); Bennett (16); Berkeley (17); Berkeley and Jackson (20, **21**); Bewley (**24, 25,** 28, 30); Boyer

[24] Those papers which contribute original research data or which are important otherwise in connection with the disease in potatoes are cited in this bibliography by numbers in bold-faced type.

Ordinary light-faced numbers refer to papers which give only conventional descriptions of the disease or contribute little or no original research data.

Throughout the following bibliographies of this paper this same practice has been observed.

(35); Carpenter (**47**, 48, **49**); Curzi (**56**); Dale (60); Dodge and Wilcox (61); Drayton (66, 318); Dufrenoy (72); Edson (**73**); Edson and Shapovalov (74, **75**); Eriksson (76); Foëx (**77**); Gram and Rostrup (78); Gravatt (81); Haenseler (89); Hardesty (95); Heald (102); Henning (104); Horne, Essig and Herms (107); Jagger and Stewart (**110**); Jardine (111); Klebahn (**113**); Köch (**115**, 116); Lindfors (119); Marchal (122); McCubbin (127); McCurry (**128**); McKay (**129**, 130, **131**, **132**); Miège (133); Oppenheimer (134); Orton (**135**, 136, **137**); Pape (140); Paravicini (139); Partridge (141); Pethybridge (**142**, **143**, **144**, **145**, **146**, **147**, **148**, **149**, **150**, **151**, **152**, 153); Picado (**155**); Quanjer (157); Quanjer, van der Lek, and Botjes (158); Rankin (161, 162, 163); Reinke and Berthold (**164**); Rosa (165); Rudolph (168); Sanford (169); Schander and Richter (**170**); Schlumberger (171, 172); Schmidt (173); Shapovalov and Link (176); Simpson (178); Spieckermann (**180**, 181); Störmer (184); Utkin (186); Van Beyma Thoe Kingma (187); van der Lek (**188**, **189**, **190**); van der Meer (**191**, **192**); van Poeteren (196, 198); Verhoeven (**200**); Weber (201); Weimer (203); Westerdijk (204); Wollenweber (212, 213, 214, 215, 216); Wollenweber and Schlumberger (219); Wormald (225); Zeller (230); Zimm (231); Zundel (232, 233). For additional references to the disease in potatoes see "Appendix," p. 350.

A Review of the Work of Ernst Hallier.—It is fitting in closing the section on potato to say a few words of the work of Ernst Hallier.[25] While the work of Reinke and Berthold correctly is acknowledged as the foundation upon which all the subsequent studies of hadromycosis are based, one is forcibly struck on reading their paper by the similarity which it bears in its main points to Hallier's on the same subject. Hallier's work is forgotten except possibly by the very few who have had the patience to wade through the flood of literature which deluged Europe and America in the eighteenth and nineteenth centuries when the attention of investigators was forcibly turned toward the diseases of *Solanum tuberosum* which were causing such unprecedented losses at the time. Hallier missed the acclaim which has rightfully fallen to Reinke and Berthold, but only by a very narrow margin.

He wrote a number of papers on a potato disease which no doubt was the one under discussion. In the earlier ones he attributed the disease to different fungi, but in his last paper which appeared just

[25] Hallier, Ernst. Die Plastiden der niederen Pflanzen. Die Kräuselkrankheit der Kartoffeln. p. 7–33. 4 pl. Fue's Verlag (R. Reisland), Leipzig. 1878.

one year before the Reinke and Berthold *opus,* he clearly summed up his earlier work and finally concluded *Pleospora polytricha* Tuls. to be the causal agent.

The great errors in his work that robbed him of the distinction that is Reinke and Berthold's, were, first, his failure to make inoculation tests with his fungus, and second, his failure to appreciate the fact that he was probably working with more than one fungus which he described collectively as *Pleospora polytricha* Tuls. Koch's postulates published just three years prior to the appearance of Hallier's paper, probably were not the great force at that time that they are today. From his descriptions and drawing, however, there can be little doubt that one of these fungi was the organism which Reinke and Berthold later proved to be the cause of the disease and named *Verticillium albo-atrum.*

Hallier made many discoveries about the disease that are outstanding. He also made some important errors, and Reinke and Berthold, probably influenced by his work, made the same errors. He described the disease in potatoes much as we would today; he noted the sharp localization of discolored tissue in the xylem elements of stems and roots. He was aware that the fungus makes its attack wholly through the roots and progresses upward in the stem and never vice versa. He noted that the leaves on affected shoots may or may not curl up exposing their under sides, also that the lower leaves turn yellow and die first. He observed that all stems of a plant do not necessarily suffer from the disease, and that the fungus is confined to the diseased stems.

He was aware that symptoms may appear in the shoots of affected plants, and particularly in shoots produced by diseased seed tubers, well in advance of the actual invasion of those parts by the fungus, and he explained the failure of so many other investigators to find the fungus in the stems upon this basis.

He realized that as the affected parts die, the fungus ceases to confine itself to the tracheae and penetrates to all parts of the surrounding tissue, eventually reaching the outer surface of the epidermis where it produces its reproductive bodies and sclerotia. He traced the mycelium through the stolons into the tubers. He believed the fungus never penetrates the latter but remains sharply localized in a little brown spot in the tissue just beneath the point of attachment to the stolon. Reinke and Berthold made this same error. But Hallier was less emphatic on this point than Reinke and Berthold, for he did recognize the possibility that the fungus might penetrate the tuber

more deeply and, he says of the fungus: "Sometimes it is visible only at the base of the stolon; in other cases, however, it penetrates a greater part of the vessels." Thirty-three years later, Pethybridge (143) verified this very important point.

Hallier appreciated that the yield from diseased plants is materially reduced and that tubers from affected plants are apt to be smaller than those of healthy plants. He experimented with tubers showing discoloration at the proximal end and proved that they give rise to diseased plants which die off very early, generally before they can form new tubers. He thus recognized two stages or forms of the disease; the first in which the plants are autochthonously infected in the soil, and the second arising when diseased tubers produced by the first-generation plants are used for seed. The disease was said to be extinguished in the second generation because of the failure of these plants to set tubers.

His many errors, particularly his peculiar ideas about the causal fungus, its method of reproduction, etc., need not be discussed here. Even in these may be found certain helpful information which Reinke and Berthold probably made use of; thus he recognized the presence of *Dauermycelium* and 'sclerotia' in the tissues and on the surface of dead potato stalks, and he appreciated the rôle they play in re-establishing the fungus in the soil, even if these bodies did not belong to the fungus he thought he was working with. His drawings, somewhat diagrammatic, leave little doubt that these sclerotia were the same as those shortly described by Reinke and Berthold and referred to the fungus *Verticillium albo-atrum.* (See plate 3.)

His symptomology led Reinke and Berthold astray. He described sharply circumscribed brown spots of increasing size on the leaves of affected plants which he erroneously associated with the disease. Also a glassy appearance and brittle consistency of the stems, particularly in those arising from diseased tubers. None of these have any connection with *Verticillium* hadromycosis. Reinke and Berthold made the same errors of observation.

It will be seen from this summary that Hallier's work closely paralleled that of Reinke and Berthold, and no doubt the latter found it a very great help in establishing the etiology of the disease on a more correct scientific basis.

Artichoke (*Cynara scolymus* L.)

In 1927 Dufrenoy (72) briefly reported isolating *Verticillium dahliae* from artichokes affected with hadromycosis. A description of the disease as it affects this variety was not given, nor were inoculation experiments to prove the pathogenicity of the organism reported.

This is the only reference to the disease in artichokes in the literature.

Beet (*Beta vulgaris* L.)

The disease was first reported in 1918 by Westerdijk (204) who had observed it for at least ten years at various places in Holland (Zeeland, on the island of Tolem, St. Maartensdijk, Ijpolder, and Haarlemmermeer, etc.) on sugar and fodder beets.

A *Verticillium* sp. identical morphologically with *Verticillium albo-atrum* was isolated from the discolored veins in the petioles and leaf blades. Artificial infection of seedlings was obtained by simply immersing seed in an aqueous spore suspension previous to planting.

The syndrome is essentially that of other plants affected with the disease, but yellow spotting of the leaves is characteristic. The spots spread and the tissue involved usually dies very quickly. The outer leaves wilt first and lie flat on the soil. Discoloration in the veins is not always readily visible owing to their narrowness.

When the disease is serious, whole fields turn yellow very quickly in the summer. The quantity production of beets is considerably reduced, especially the yield of leaves, which are used for fodder.

Van der Meer (191) reports *Verticillium dahliae* Kleb. also to be the cause of hadromycosis in beets.

Bibliography.—Rudolph (168) ; van der Meer (191) ; van Poeteren (**197**) ; Westerdijk (**204**) ; Wollenweber (216).

Chayote (*Sechium edule* Swartz.)

See "Tobacco" (p. 311).

Cucumber (*Cucumis sativus* L.)

In 1917 Lindfors (119) described a typical hadromycosis of cucumbers and proved the causal agent to be *Verticillium albo-atrum* by making suitable inoculation experiments. He regarded the disease as of no consequence but reported losses amounting to 50 per cent of the crop in individual cases.

In 1918 and 1919 van der Lek (188, 189) reported the results of experiments started in 1916. He mixed pure cultures of the fungus into sterile soil in pots and then planted young cucumber plants in them. Suitable controls were provided. The experiment was repeated several times, the number of plants used each time varying from six to fourteen. His results amply confirmed Lindfors' work.

The disease thus far has been observed almost exclusively in greenhouses and coldframes in Europe, particularly in Sweden, Holland, Denmark, and England. It has never been reported in America.

The syndrome is essentially that described under "Description of *Verticillium* Hadromycosis" (p. 210). In addition to the usual disease picture, van der Lek (190) also described "wedge-shaped necroses" in the leaves due to the invasion of the parenchyma from the veins by the fungus.

The cross-inoculation experiments of Bewley (25, 28), and van der Lek (188, 189), are of interest. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

Bibliography.—Beaumont (316); Bewley (23, **24**, **25**, **28**, 30); Boyer (35); Curzi (56); Dufrenoy (72); Gram and Rostrup (80); Lindfors (**119**); Pape (140); Pethybridge (153); Utkin (186); van der Lek (**188**, **189**, **190**); van der Meer (191, 192); Weber (201, 202); Wollenweber (216).

Eggplant (*Solanum melongena* L.)

In 1913, Wollenweber (213, 214) briefly reported the results of successful inoculation experiments on eggplant with *Verticillium*. In 1914 Orton (136) stated that he and Wollenweber had observed eggplants at Hood River and Medford, Oregon, and at Santa Ana, California, autochthonously infected by the fungus. Haenseler in New Jersey has given more attention to the disease in this plant than any one else.

The syndromal characteristics are essentially those described under "Description of *Verticillium* Hadromycosis" (p. 210). The more obvious symptoms are stunting, discoloration of the xylem, and gradual desiccation of the leaves from below upward. There is no decay of the fruit or other portions of the plant below or above ground. According to Jagger and Stewart (110), the fungus may be isolated from the fibro-vascular bundles of the fruit, however.

Varietal Resistance.—Haenseler (87, 92, 93) considers the Italian varieties the most resistant. Unfortunately they are unsuited to com-

mercial requirements. He reports the Black Beauty variety as particularly susceptible. The New York Spineless, New York Improved, and Florida Highbush show slight resistance. Guba (321) reports the New York Purple to be very susceptible.

Haenseler (253) found wild eggplant (*Solanum floridanum*) to be too susceptible to be of value in breeding for resistance.

Jagger and Stewart (110) report an experiment in which all obtainable strains and varieties of cultured eggplants were grown in a field severely infested with *Verticillium*. A total of twenty-eight varieties were represented, the seed being obtained from America, France, England, and China. From three to eight plants of each were grown. Every plant showed marked symptoms of the disease and made only a stunted growth. (See "Horse Nettle," p. 327, and "Scarlet Eggplant," p. 332.)

Cross-Inoculation Experiments and Culture Studies.—The works of Bewley (24, 25, 28), Jagger and Stewart (110), Haenseler (83, 84, 88, 90, 93, 94), Carpenter (47, 49), Zimm (231), Weimer (203), and Martin (124), demonstrate the very close relationship, if not the identicalness of the species of *Verticillium* which attacks eggplant and a wide range of other varieties. See "Cross-Inoculation Experiments with *Verticillium* Species (p. 235) for a further discussion of this subject.

According to various authors a typical hadromycosis may be produced in the eggplant by several species of *Verticillium,* namely, *V. tracheiphilum* Curzi (54), *V. ovatum* Berkeley and Jackson (20, 21), *V. albo-atrum* R. and B., Wollenweber (213, 214); Carpenter (47, 49); Bewley (24, 25, 28), and many others. Also *V. dahliae* Kleb., if this strain is to be regarded as a separate species as claimed by Klebahn (113). See "Discussion of *Verticillium* Species Associated with Hadromycosis" (p. 244) for further discussion of the relationship of these fungi.

Bibliography.—Bennett (16); Berkeley and Jackson (20, 21); Bewley (**24**, **25**, 28, 30); Boyer (35); Carpenter (47, **49**); Cook (53); Curzi (54); Dodge and Wilcox (61); Dufrenoy (70, 72, 319); Edson and Shapovalov (74); Giddings (323); Guba (321); Gravatt (81); Haenseler (83, **84**, 86, **87**, 88, **89**, **90**, **91**, 92, 93); Hardesty (95); Harter and Field (101); Jackson (109); Jagger and Stewart (**110**); Lipman (120, 121); Martin (124, 125, 126); Orton (136); Osmun (138); Rankin (162, 163); Rudolph (168); van der Lek (188, 189); van der Meer (191, 192); Weimer (203); Wollenweber (**213**, **214**, 216); Zimm (**231**). See also "Appendix" (p. 350).

Ginseng (*Panax quinquefolius* L.)

In 1904, van Hook (194) described the disease in New York State. He attributed it to *Acrostalagmus albus* Pr.

In 1910, Rankin (159), probably unfamiliar with van Hook's work, again described the disease and named the causal organism *Acrostalagmus panax* Rankin, without giving a technical description of it or reasons for changing the name.

In 1912, Whetzel and Rosenbaum (206) reported the disease in New York, Pennsylvania, Michigan, Ohio, New Jersey, Wisconsin, Kentucky, and Tennessee. Losses as great as 20 per cent of the crop due to killing of the plants are attributed to it.

Several other writers have since reported the disease, but no one seems to have conducted inoculation experiments to prove the pathogenicity of the fungus. Similarly, no cross-inoculation experiments with *Verticillium* from other varieties have been made.

The syndrome is essentially that observed in other plants affected with the disease, the xylem presenting a characteristic brownish red discoloration.

Bibliography.—Carpenter (47, 49); Dufrenoy (319); Haenseler (89); Rankin (**159**); Van Hook (**194**); Whetzel and Rosenbaum (**206**); Whetzel, Rosenbaum, Brann, and McClintock (**207**); Wollenweber (216).

Graeskar[26] (*Cucurbita* sp.)

In 1925 Gram and Rostrup (80) briefly reported the disease in *Graeskar* in Denmark, without giving descriptions or experimental data. The plants observed were attacked in May, and the disease was again observed in September. Many petioles, shoots, or whole plants were killed. The stems finally became black and covered with a gray-white mould.

No other reference to the disease in this variety has appeared in the literature.

Horse-Radish (*Radicula armoracia* [L.] Robbins.)

In 1923, Pötschke (156) briefly reported isolating *Verticillium albo-atrum* R. and B. from horse-radish. He claims to have established the pathogenicity of the organism with laboratory and greenhouse experiments.

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[26] The meaning of the term *Graeskar* is not clear. Danish-English dictionaries define graeskar as gourd, pumpkin, vegetable marrow (*Cucurbita ovifera*).

Blattný (32) reports the disease to be widespread in Bohemia in this species, which forms an important item of cultivation. He attributes the increase in incidence and severity of the disease to the fact that the crop is seldom rotated, horse-radish being grown frequently for periods as long as thirty or forty years on the same land, and in some instances for over one hundred years. He recognizes varietal resistance. He attributes the disease to *Verticillium dahliae* Kleb. rather than to *V. albo-atrum* R. and B., although in the main he agrees with Pötschke regarding the syndromal characteristics, which are those generally observed in other varieties.

Van der Meer (191) lists the horse-radish in her *Verticillium* host table giving Pötschke as reference. No other writers have reported the disease in this species.

Kidney Bean (*Phaseolus vulgaris* L.)

In 1922, Averna-Saccá (10) reported *Verticillium* hadromycosis of tobacco in Brazil. He states that *Verticillium albo-atrum* R. and B. also was found attacking *feijao guando* (kidney bean). No experimental data or descriptions of the disease in beans are given. No other writer reports the disease in this species. (See "Tobacco" (p. 311).

Muskmelon (*Cucumis melo* L.)

In 1918, van der Lek (188) reported a hadromycosis of melons due to *Verticillium albo-atrum* R. and B. Since his paper appeared the disease has been recognized in melons in England (30), Denmark (80), and France (67, 69). The disease never has been reported in this species in America, although Bennett (16) reports that a field of raspberries planted on soil which previously had been planted to melons for several successive years suffered a severe attack of the disease. The inference given is that the melons propagated and disseminated the fungus in the soil.

Van der Lek (189) states that melons and cucumbers are more resistant to the disease than potatoes.

Dufrenoy (69) has described the pathologic histology of melon vines suffering from the disease and reports (72) that affected plants may die rapidly.

Specimens of diseased melon vines were submitted to the Deciduous Fruit Field Station recently. The plants were affected with a typical hadromycosis and *Verticillium* sp. was isolated in pure culture from them. The grower of the plants reported the Persian and Gold Nugget varieties to be susceptible to the disease, the former particularly so.

The syndromal characteristics are essentially those observed in other truck crop plants affected with *Verticillium* hadromycosis. See "Description of *Verticillium* Hadromycosis" (p. 210).

Bibliography.—Bennett (16); Bewley (30); Curzi (56); Dufrenoy (67, **68**, **69**, 72); Gram and Rostrup (80); van der Lek (**188**, 189); van der Meer (191); Wollenweber (216).

Okra (*Hibiscus esculentus* L.)

The identity of the disease was established by Wollenweber (213, 214), who isolated the fungus in 1913 from autochthonously infected plants grown in South Carolina.

Carpenter (47, 49) isolated the fungus from specimens from Alabama, and from Middle River, California. Haenseler (83, 88, 89, 90, 92, 93), Orton (136), Carpenter (47, 49), and Martin (124) report the disease to be of serious consequence in New Jersey. According to Haenseler (89) as many as 95 per cent of the plants in fields in that state have been attacked.

No writer has given a detailed description of the disease, but presumably the syndrome is essentially that described under "Description of *Verticillium* Hadromycosis" (p. 210).

The observations, cross-inoculation work, and cultural studies of Haenseler and Carpenter are of interest. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235) for further discussion of cross-inoculation studies.

Bibliography.—Carpenter (**47**, **49**); Cook (52); Edson and Shapovalov (74); Haenseler (83, 88, **89**, 90, 92, 93); Jagger and Stewart (110); Martin (124, 125); Orton (136); Rankin (162, 163); Rudolph (168); van der Lek (188, 189); Wilson (209); Wollenweber (**213**, **214**, 216); Woodruff (220). See also "Appendix" (p. 350).

Pepper (*Capsicum* sp.)

Sweet pepper.....*Capsicum annum* L.

In 1921, Bewley (24) reported successful inoculation of pepper plants (*Capsicum* sp.) with *Verticillium albo-atrum* from tomatoes. The following year (25) he again reported similar experiments. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235) for further discussion of cross-inoculation experiments.

In 1922, Wollenweber (216) included *Capsicum* sp. in a host list of *Verticillium albo-atrum*. Descriptions and experimental data were not given. Van der Meer (191) and Dufrenoy (72) citing Wollen-

weber as reference, list the species as *C. frutescens* Willd. for reasons not given.

In 1925, Curzi (54, 55) simultaneously published two reports of a hadromycosis of pepper plants (*Capsicum annum* L.) due to *Verticillium tracheiphilum* n. sp. He proved the pathogenicity of the organism with suitable experiments. The fungus is said to be widely scattered in Italy and is capable of attacking eggplants.

The syndrome is essentially that given under "Description of *Verticillium* Hadromycosis" (p. 210). Curzi reports a decay at the base of diseased plants grown in humid conditions. The disease in peppers has never been definitely reported in America.

Bibliography.—Berkeley and Jackson (21); Bewley (**24, 25,** 28, 30); Curzi (**54, 55**); Dufrenoy (72); Haenseler (84, 93); van der Meer (191); Wollenweber (**216**).

Rhubarb (*Rheum rhaponticum* L.)

The disease was briefly reported in rhubarb by Wormald (226, 227) in 1928. The syndromal characteristics are essentially those observed in other plants affected with the disease.[27] No other writers have reported the disease in rhubarb.

Salsify (*Tragopogon porrifolius* L.)

In 1918, Jagger and Stewart (110) reported having isolated a *Verticillium* sp. from diseased salsify growing near Rochester, New York. They made no inoculations to prove the pathogenicity of the fungus. Their description of the disease is very brief, but the syndrome apparently is identical with that presented by various other plants affected with *Verticillium* hadromycosis. The discoloration in the xylem is described as a greyish-brown. See "Description of *Verticillium* Hadromycosis" (p. 210).

No other workers have reported the disease in salsify, although references to Jagger and Stewart's work are made.

Bibliography.—Dufrenoy (72); Haenseler (89); Jagger and Stewart (**110**); Rankin (162, 163); van der Lek (189); van der Meer (191).

Tomato (*Solanum lycopersicum* Trn.)

Bonny Best tomato.....*Lycopersicum esculentum* Mill.
Currant tomato.....*Lycopersicum pimpinellifolium* Dunal.

[27] In a letter, R. V. Harris, in charge of *Verticillium* disease investigations at the East Malling Research Station, Kent, England, describes the disease as a true hadromycosis. The fungus is said to resemble *V. albo-atrum* but culturally it is distinct from the species associated with the disease in hops in England.

The disease was first definitely reported on the Bonny Best tomato (*Lycopersicum esculentum* Mill.) and on the Currant tomato (*L. pimpinellifolium* Dunal.) by Jagger and Stewart (110) in January, 1918, and on *Solanum lycopersicum* Trn. by van der Lek (189),[28] in November of the same year. These writers established the pathogenicity of the fungus by making inoculations.

Since the above papers appeared, the disease has been reported in widespread localities in the United States and Canada, also throughout Europe including the British and Channel Islands wherever tomatoes are grown.

Bewley (25, 30) regards the disease described on tomatoes in England by Massee in 1896, and attributed to a *Diplocladium* by him, to be identical with hadromycosis.

The syndromal characteristics are essentially the same as those observed in other species, especially the potato. See "Description of *Verticillium* Hadromycosis," (p. 210). Figures 8 and 9 show the contrast between a healthy and diseased plant. Figure 6 (p. 221) shows the characteristic internal discoloration of tomato stems affected with the disease.

Reinke and Berthold described brown spots or lesions in the cortex of potato stems below the ground. Bewley (24, 30) has reported similar lesions in the cortex of tomato stems: "The fungus destroys the cortex at the point of entrance, and, entering the wood passes up the stem. Here it is found solely in the woody parts." Neither author has supplied a photograph of these lesions.

In California these brownish-black spots are commonly found on tomato stems below ground, and not infrequently such lesions are so numerous and deep that they alone are probably sufficient to weaken the plant greatly. The fungus is easily isolated from the tissue immediately contiguous to these lesions. Figure 4 (p. 217) shows the lesions produced on the underground portions of the stems of tomato. Such lesions may develop on the larger secondary roots also.

The veins of the leaves of affected tomato plants frequently develop a pronounced purplish color. Since the leaves tend to roll upward along the midrib and expose the lower surface, these discolored veins are more or less exposed and give the affected plant a dark or dull appearance.

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[28] In a footnote van der Lek gives the credit of discovering the disease in tomatoes in Holland to Schoevers, who was said to have isolated the fungus from diseased plants in 1916. Schoevers apparently never published a report of his work.

Bewley (24, 30) reports a soft rot of tomato fruits caused by *Verticillium albo-atrum,* which is said to penetrate the fruits by way of the stems. Under California conditions, tomato fruits are never affected with rots which can be attributed to *Verticillium.*

Losses Due to Verticillium Hadromycosis of Tomatoes.—Writers say very little about the losses occasioned by this disease in tomatoes.

Fig. 8. A healthy, vigorous tomato plant with some of its normal, unripe fruit removed. San Jose Canner variety.

The picture of this plant was taken for the sake of contrast with the plant shown in figure 9. Both plants were photographed from approximately the same distance. Note the well-developed leaves and firm shoots of the healthy plant.

If not infected too early in the season, or, if infected early and the attack is not severe, affected plants may produce a satisfactory yield. Bewley (24, 30) states that the disease "is the cause of considerable financial loss to the industry." Actual losses occasioned by the disease in California are unknown, but in certain communities they have been very heavy undoubtedly.

The fruits on vines affected by the disease in an advanced stage are generally smaller than those on healthy plants of the same age, and in cases of very severe attack, too small and inferior to be worth picking.

Plants affected early in the season may die without having produced marketable fruit. Plants affected after maturity may die or cease to produce marketable fruit much earlier than healthy plants. The canning season in California extends from September 15 to November 1, but not infrequently the canneries continue to accept fruit of satisfactory quality until a much later date or until the vines have been destroyed by frost. Plants with *Verticillium* hadromycosis ordinarily have died or have ceased to produce satisfactory fruit long before this time.

Fig. 9. A tomato plant, San Jose Canner variety, in an advanced stage of *Verticillium* hadromycosis. Note the poorly developed, curled leaves and wilted stems.

The fungus was isolated in pure culture from this plant after the picture was made.

In 1925 in one large field in the Santa Clara Valley, picking operations were stopped in early September because of the very inferior quality of so much of the fruit. Investigation showed at least 90 per cent of the vines to be affected with *Verticillium* hadromycosis.

Varietal Resistance in Tomatoes to Verticillium Hadromycosis.—Bewley (24, 25, 28, 30) considers that marked varietal resistance and susceptibility exists. He states (24):

> Plants grown 'hard' are more susceptible to the disease than the softer succulent types, and consequently varieties like Kondine Red show a strong susceptibility. Plants which have been starved in the early stages or suffered a prolonged check show a high percentage of the disease.

He further concluded from his experiments (25) that the variety Manx Marvel is "practically immune" and that Bide's Recruit is "highly resistant."

Under California field conditions,[29] neither Manx Marvel nor any of the other commoner varieties grown in this country have shown any particular resistance to the disease.

The following varieties are known to be susceptible: Kondine Red (24); Comet (25, 30); Bide's Recruit (25); Ailsy Graig, Tuckwood, Westland (191, 192); Santa Clara Canner, Marvana, Marvelosa, Globe, Norduke, Norton, Columbia, San Jose Canner, Marglobe, Dwarf Champion, Stone, Pritchard's Marvel, Earliana, Penn. State Earliana, Yellow Egg and Manx Marvel (Shapovalov and Rudolph).[30]

Species of Verticillium Reported Producing Hadromycosis in the Tomato.—Van der Meer (191) states that both *Verticillium alboatrum* and *V. dahliae* produce hadromycosis in the tomato.

Pritchard and Porte[31] have described a 'collar rot' in tomatoes due to a new species of *Verticillium* which they have named *V. lycopersicum.* This disease is not a true hadromycosis. It is unknown in California and the causative fungus is very dissimilar in appearance to the species of *Verticillium* associated with hadromycosis in the tomato and other varieties.

Berkeley and Jackson (20, 21), authors of *V. ovatum,* which is said to produce a typical hadromycosis in raspberry plants, regard the tomato as susceptible to attack by their fungus.

A discussion of the taxonomic relation of the several putative species of *Verticillium* may be found under "Discussion of *Verticillium* Species Associated with Hadromycosis" (p. 244).

Bibliography.—Bennet (16); Berkeley (17); Berkeley and Jackson (20, **21**); Bewley (23, **24**, **25**, 27, **28**, **29**, **30**, 317); Boyer (35); Brittlebank (36); Bryan (38); Dodge and Wilcox (61); Dufrenoy (72); Gram and Rostrup (79, 80); Gravatt (81); Haenseler (84, 89, 93); Hardesty (95); Horne, Essig, and Herms (107); Jagger and Stewart (**110**); Pape (140); Pethybridge (153); Rankin (162); Rosa (166); Rudolph (44, 45, **167**, 168); Simpson (178); Taylor (185);

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[29] M. Shapovalov, Office Horticultural Crops and Diseases, United States Department of Agriculture, and I are conducting certain experiments at present under field conditions with a view to selecting a variety of *Verticillium*-resistant tomato which will meet with canning requirements. Thus far we have found little if any difference in the susceptibility of the various varieties used in the experiments. All varieties grown in naturally infected soil apparently may be affected by the disease with equal severity.

[30] Mentioned for the first time in this paper.

[31] Pritchard, F. J., and W. S. Porte. Collar rot of tomato. Jour. Agr. Res. 21(3):179–184. 5 pl. 1921.

Utkin (186); van der Lek (**189**, **190**); van der Meer (**191**, **192**); van Poeteren (195, 196); Weber (201, 202); Williams (208); Wollenweber (216). See also "Appendix" (p. 350).

Udo (*Aralia cordata* Thunb.)

In 1923, Weimer (203) described a hadromycosis of the udo due to *Verticillium albo-atrum*. His paper is the only one which has appeared to date describing the disease and giving experimental data. He proved the pathogenicity of the fungus with numerous controlled experiments both in the field and in the greenhouse, using plants of various ages.

The syndrome is essentially that observed in other plants affected with the disease. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235) for discussion of cross-inoculation experiments.

Bibliography.—Van der Meer (191); Weimer (**203**). See also "Appendix" (p. 350).

Watermelon (*Citrullus vulgaris* Schrad.)

According to Wollenweber (216), *Verticillium albo-atrum* attacks the watermelon in Oregon "under certain conditions." His report is very brief and not substantiated either by descriptions of the disease or by experimental data. The disease has never been reported in this species by any other writers.

Van der Meer (191) and Dufrenoy (72) include watermelon in their host tables, giving Wollenweber's paper as their source of information.

FRUIT TREES AND NUTS

Almond (*Prunus communis* Fritsch)

In 1923, Czarnecki (58) reported isolating a *Verticillium* from almonds in California which she regarded as identical with that attacking apricots. She made no cross inoculations. The disease has been observed for many years in California. In 1927, Dufrenoy (72) reported the disease in almonds in France.

The almond, especially when young, is very susceptible to attack and various commercial varieties are affected.

The syndrome is essentially that observed in fruit trees and woody plants affected with the disease. See "Description of *Verticillium* Hadromycosis" (p. 210).

Bibliography.—Czarnecki (**58**); Dufrenoy (71, **72**); Rudolph (168). See also "Appendix" (p. 350).

Apricot (*Prunus armeniaca* L.)

In 1916, Phillips (154) reported the disease known as 'black heart' of apricots before the Pacific Division of the American Phytopathological Society.

In 1917, Czarnecki (57) presented the results of her experiments on the "black heart disease of apricots" before the same body. She did not publish her abstract.

In 1923, Czarnecki's paper (58) appeared describing her experiments and definitely establishing proof of the cause of the disease. She referred to the organism responsible for the disease as a *Verticillium* species.

In 1927, Berkeley (18) briefly reported the disease in apricots in Canada and gave the results of successful inoculation experiments.

In 1927, Dufrenoy (67, 72) reported the disease in apricots over a wide area in France. He found that apricot grafts on affected prune stocks suffer severely from the disease and may even die. Infection of the grafts takes place through the prune stock, although the wood of the latter is said to show less discoloration than that of apricot.

The syndrome is essentially that observed in other varieties affected with the disease. See "Description of *Verticillium* Hadromycosis" (p. 210). Figures 1 (p. 213) and 3 (p. 215) show the effect of the disease in apricot trees.

Van der Meer (191) has referred the species of *Verticillium* attacking apricots in California to *V. dahliae* Kleb. Similarly Dufrenoy (72) has referred the *Verticillium* on apricots in France to this species. The taxonomic position of *V. dahliae* Kleb. is further discussed under "The Relation Between *Verticillium albo-atrum* R. and B. and *V. dahliae* Kleb." (p. 247).

The disease is widespread in California at present and in certain years occasions severe losses in young orchards. Under certain conditions every tree in an orchard may be attacked. While comparatively few trees die, many of them are retarded in growth or badly deformed as the result of the killing of the main branches by the disease. Eventually the trees outgrow their susceptibility to the disease to a large degree but present a poor shape and general appearance as the result of attacks in early life.

The disease has been observed in the Moorpark and Blenheim varieties, the latter being particularly susceptible to attack.

For cross-inoculation experiments with the *Verticillium* from apricot and other varieties see "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

Bibliography.—Ann. Rept. Univ. Calif. (42, 44); Berkeley (**18**); Czarnecki (57, **58**); Dufrenoy (67, **68**, 72, 319); Horne, Essig, and Herms (107); Phillips (154); Rudolph (**167**, 168); van der Meer (191). See also "Appendix" (p. 350).

Cherry (*Prunus* spp.)

Sour cherry.....*Prunus cerasus acida* Ehrh.
Morella cherry.....*P. cerasus austera* Ehrh.
Mahaleb cherry.....*P. mahaleb* L.
Mazzard cherry.....*P. avium* L.

The cherry was the first economic fruit tree definitely reported in the literature to be subject to *Verticillium* hadromycosis.

In 1918, van der Lek (189) reported the disease in sour cherries. He isolated a *Verticillium* resembling *V. albo-atrum* R. and B. from affected trees. Experimentally he found the fungus to be pathogenic to cucumbers and potatoes. He does not report making inoculations in cherries to determine its pathogenicity in this species.

In 1925, van der Meer (191, 192) reported isolating *Verticillium albo-atrum* R. and B. from the following varieties of sour cherries: Meikers, Bieskers, Eijsdensche kers, Spaansche kers; and *V. dahliae* Kleb. from the variety Hedelfinger Riesen and from Morello and Mahaleb cherries. See "The Relation Between *Verticillium albo-atrum* R. and B. and *V. dahliae* Kleb." (p. 247).

In 1926, an anonymous writer (4) reported the disease in Mazzard cherries in Czecho-Slovakia.

Van der Meer (191, 192) conducted many different inoculation experiments with cherries, using pure cultures of *Verticillium albo-atrum* from cherry and potato and *V. dahliae* from potato. She used a large number of plants, and her inoculations were conducted under strictly aseptic conditions with proper controls. Her cross-inoculation experiments are of particular interest. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

The disease has been reported in cherries in Denmark, France, Corsica, and Holland. It has never been reported in America on cherries of any kind.

Bibliography.—Anonymous (4); Bally (13); Berkeley and Jackson (21); Dufrenoy (67, **72**); Gram and Rostrup (79, 80); Pape (140); van der Lek (**189**); van der Meer (**191**, **192**); van Poeteren (196, 199); Wollenweber (216).

Peach (*Prunus persica* Sieb. and Zucc.)

In 1922, Haenseler (83) isolated a *Verticillium* from young peach trees which were affected with a typical hadromycosis in New Jersey. He considered the fungus identical with *V. albo-atrum* R. and B.

The work done on the disease in this plant is very meager. Haenseler (83, 88, 90) and Rudolph (167) apparently are the only ones who have made cultural studies of the fungus from peach or inoculation tests, etc. The cross-inoculation experiments of Haenseler and Rudolph are reported under "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

Haenseler (90) was unable to infect peach seedlings with *Verticillium* from peach and concluded that special conditions are essential to bring about infection.

The disease is widespread in peach in California, particularly in the cooler, coast counties. The syndrome is essentially the same as that observed in other species affected with the disease.

Bibliography.—Bennet (16); Berkeley and Jackson (21); Curzi (56); Dufrenoy (67, 72, 319); Haenseler (83, 85, **88**, 89, **90**); Martin (124); Rudolph (**167**, 168); van der Meer (191). See also "Appendix" (p. 350). See "Flowering Peach" (p. 325).

Plum, Prune (*Prunus* spp.)

Common plum.....*Prunus domestica* L.
Myrobalan plum.....*P. cerasifera* Ehrh.
St. Julian plum.....*P. domestica* L. var. *insititia* Bailey.

In 1923, Czarnecki (58) reported the disease in California on imported myrobalan seedlings. She regarded the *Verticillium* which she isolated from this variety as identical with that from apricots but made no cross-inoculations to prove the point.

In 1926, Rudolph (167) reported successful inoculation experiments with myrobalan seedlings. He also reported successful cross-inoculation experiments on myrobalan seedlings with *Verticillium* from tomato, apricot, peach, and raspberry. See "Experiments at the Deciduous Fruit Field Station" (p. 240).

In 1927, Dufrenoy (72) reported the disease in *Prunus domestica* L., and *P. cerasifera* Ehrh., also in the St. Julian and the Reine-Claude plums in France.

The disease has been observed in commercial varieties of prunes in California for many years. Young French and sugar prunes may suffer severely, but ordinarily they are more resistant than the apri-

cot. In this connection Dufrenoy (72) has observed that apricot grafts on plum stocks may be killed by the disease while the stocks upon which they are borne survive, at times apparently affected by the disease only in a minor degree.

In California myrobalan seedlings are highly susceptible. They may be killed or rendered unfit for budding purposes in the nurseries in the San Francisco Bay region.

The syndrome is identical with that generally observed in woody plants affected with the disease. See "Description of *Verticillium* Hadromycosis (p. 210).

Bibliography—Czarnecki (**58**); Dufrenoy (67, 72); Gram and Rostrup (79, 80); Rudolph (**167**, 168).

Walnut (*Juglans* sp.)

In 1927, Dufrenoy (67, 70) briefly reported isolating a *Verticillium* from walnut trees apparently affected with hadromycosis. The species of walnut affected was not mentioned.

The syndromal characteristics are essentially those observed in other trees affected with the disease. In addition to the usual characteristics of the disease, lesions are said to develop on the bark of the collar just below the ground level. The bark over the affected area may slough off exposing the blackened wood beneath.

No other writers have reported the disease in walnuts.

FOREST TREES AND MISCELLANEOUS ECONOMIC PLANTS

Banana (*Musa sapientum* L.)

See "Tobacco" (p. 311).

Cacao (*Theobroma cacao* L.)

In 1910, Guéguen[32] described a disease of cacao pods at San Thomé which he attributed to *Acrostalagmus vilmorinii* var. *cacao* Guéguen. In 1918, Carpenter (49) referred this variety to the genus *Verticillium*.

The disease in no way resembles a hadromycosis, and its discussion has no place in this paper. It is mentioned here because occasional writers discussing *Verticillium albo-atrum* refer to the cacao tree as a host plant.

[32] Guéguen, F. Sur une maladie du fruit du cacaoyer produite par une mucédinée et sur la mécan de l'infection. Paris Soc. Biol. **68**:221–222. 1910.

As described by Guéguen, the fungus attacks the placental column, funicles, and the muscilagenous pulp of the pods to which it gains entrance through the tiny holes made by a scolytid beetle. Having gained entrance to the pod, the seeds are attacked by the insect in such a way that the radicles are destroyed.

The fungus produces a sour, odorous decay in the pod and penetrates the seed, passing around the folds of the cotyledons. It was never observed to attack the material of the cotyledons itself although they gradually turn black owing to the oxidation of the tannins present. The fungus apparently is incapable of penetrating the integument of the kernels, although the latter are covered with a fuligenous mold which renders the product unfit for commercial purposes.

Averna-Saccá (10) briefly reports *Verticillium albo-atrum* as a parasite of cacao trees in Brazil. No descriptions or experimental data are furnished. See "Tobacco" (p. 311).

Coffee (*Coffea arabica* L.)

In 1926, Averna-Saccá (11) reported *Verticillium albo-atrum* R. and B. as a parasite of coffee berries in Brazil. Of the disease, which in no way resembles a hadromycosis, he says:

> Just now it is developing in the coffee beans penetrated and more or less spoiled by *Fusarium* or other micromycetes.
>
> . . . . . .
>
> The fruits show at times on the pericarp or in the contracted, blackened albumin an efflorescence of sandy appearance, delicate, first whitish then ferruginous, which grows and extends with certain rapidity, especially in humid surroundings, covering all parts of the attacked organ. Insinuating itself between the broken or contracted tissue it produces plaques or pseudo-membranes, white or ferruginous, formed by mycelium with conidiophores and conidia.
>
> If in the destruction of the seed only the *Verticillium* is responsible, then the albumin contracts and blackens, shrivels, but if one or another of the above-mentioned pathological factors enter, then the morbid manifestations become confused with those previously described.

A description of the fungus follows accompanied by drawings too diagrammatic to permit of identifying the organism, which in all probability is not *Verticillium albo-atrum* R. and B. or its closely related forms. See "Tobacco" (p. 311) for a further discussion of this subject.

Bally (13) recently reported a hadromycosis of coffee plants in Sumatra and Java. Among other fungi, he isolated *Verticillium lateritium* from the ducts of affected plants. He did not establish the pathogenicity of this species for coffee.

Cotton (*Gossypium herbaceum* L.)

In 1914, Carpenter (47) briefly reported a spontaneous wilt of two cotton plants at Arlington, Virginia, which he attributed to *Verticillium albo-atrum*. No descriptions or experimental data were given. He expressed the opinion that *Verticillium* may be responsible for some of the damage to this plant in the south which is now attributed to *Fusarium vasinfectum*.

In 1918, Carpenter (49) briefly reported successfully inoculating cotton plants with *Verticillium* from okra. Bewley (24, 25) reports similar success with *Verticillium* from tomato. See also "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

The descriptions of the disease in cotton are very meager and unsatisfactory and no pictures have appeared. Bewley (24, 25) merely reports a stunting of the plants and desiccation of the leaves thirty-five days after inoculation. Carpenter (49) reports 80 per cent of twenty plants inoculated showed symptoms of wilt in fourteen days. He further states that *Fusarium* wilt and *Verticillium* wilt are indistinguishable except by cultural methods.[33]

Bibliography.—Bewley (**24**, **25**, 28, 30); Carpenter (**47**, **49**); Dufrenoy (319); Haenseler (89); Rankin (162, 163); van der Lek (189); van der Meer (191). See also "Appendix" (p. 350).

Elm (*Ulmus* spp.)

English elm.....*Ulmus campestris* L.
Belgian elm.....*U. campestris* L. var. *latifolia* Gillekins.(?)[34]
Monument elm...*U. campestris* L. var. *monumentalis* Ruiz.(?)
Wheatley elm.....*U. campestris* L. var. *wheatleyi* Simon-Louis.(?)
Scotch elm.....*U. montana* With.(?)

In 1920, the annual report of the Phytopathological Service at Wageningen, Holland, for 1919 (2) appeared, giving the following brief report of *Verticillium* hadromycosis of elms. This is the earliest report of the disease in this variety:

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[33] In 1929, C. D. Sherbakoff briefly described the disease in cotton. (Phytopath. **19**(1):94. 1929. Also, Univ. Tennessee Agr. Exp. Sta. Cir. **24**:2. 1929.) In the article in Phytopathology, an attempt to distinguish between cotton wilt due to *Fusarium vasinfectum* and that due to *Verticillium albo-atrum* has been made. The descriptions are contradictory, however, particularly with reference to the discoloration observed in the affected plants.

[34] Writers frequently omit the name of the author of the species of plant with which they have associated the disease. The authors of the *Ulmus* species listed above are probably correct, but in the absence of absolute proof a question mark has been placed after the author's name.

Verticillium (probably *albo-atrum*) was noticed in the branches of *Ulmus wheatlei* at Hoeven and caused there brown spots in the wood. The disease was very destructive, because all the trees attacked died. The disease was also observed in *Ulmus campestris.*

In 1921, Bewley (24) reported successfully inoculating young elms with *Verticillium* from tomato. In 1922, Spierenburg (182) reported isolating a *Verticillium* from *Ulmus monumentalis* and *U. campestris latifolia.* From the disease picture described it would seem that the trees suffered from hadromycosis. The author made no inoculation experiments with *Verticillium* and was reluctant, therefore, to draw final conclusions as to the etiology of the disease. In 1928, Stapp (183) reported isolating *Verticillium albo-atrum* from a seedling of *Ulmus montana.*

It has never been reported in North America.

The disease runs a severe course in elms, the affected trees or limbs often dying. The syndrome is essentially that observed in other varieties of woody plants affected with the disease.

Bibliography.—Anonymous (2); Bewley (**24**, 25, 28, 30); Buisman (40); Dufrenoy (72); Spierenburg (**182**); Stapp (183); van der Meer (191, **193**).

Hop (*Humulus lupulus* L.)

The annual reports of the East Malling Research Station, Kent, England, for 1924, 1925, 1926, and 1927 briefly mention the disease in hops. In 1927, Harris (99) gave a description of the disease and reported the results of his laboratory experiments. Since this paper appeared, Harris has succeeded in proving, with suitable inoculation experiments, the pathogenicity of the *Verticillium* which he originally isolated from diseased bines.[35]

Wormald (225) reports the *Verticillium* from hops to be pathogenic to potatoes. See also "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

The syndromal characteristics, namely, discoloration of the xylem of the roots and stems and a gradual dying of the leaves from the bottom of the plant upward, are essentially the same as those observed in other species attacked by the disease. One or more bines in a hill may be affected. Those diseased are said to pull away from the main crown much easier than healthy ones.

The Fuggles variety is noticeably susceptible. In one garden approximately 40 per cent of the entire planting was diseased. Plants of the Tutsham variety show greater resistance.

[35] Personal letter.

Zattler (229) reported the disease in hops in Bavaria, and Blattný (33) in Czecho-Slovakia in 1928.

Bibliography.—Blattný (33); Harris (**99**); Wormald (221, 222, 223, 224, **225**, 228); Zattler (229).

Maple (*Acer* spp.)

Norway maple	*Acer platanoides* L.
Schwedler's Norway maple	*A. platanoides* L. var. *schwedleri* Kock.
Red maple	*A. rubrum* L.
Silver maple	*A. saccharinum* L.
Box elder	*A. negundo* L.
Sugar maple	*A. saccharum* Marsh.
Sycamore maple	*A. pseudoplatanus* L.
Japanese red maple	*A. palmatum* Thunb. var. *rubrum* Schwerin.

In 1914, Rankin (160) first reported the disease in hard maples growing near Claverak, New York, and attributed it to an *Acrostalagmus* sp. In 1917, Zimm (231) referred the organism to the genus *Verticillium* and verified the observations of Rankin. He successfully inoculated the Norway, sugar, and red maple. In 1920, the disease was first reported on *Acer* sp. in Europe at Laren, Holland (2). In 1921, Bewley (24) reported having successfully inoculated the sycamore maple in England.

At present the disease is reported to occur in a great area of the United States bounded on the south by and including Tennessee and North Carolina, and on the west by and including Illinois, Wisconsin, and Michigan. Sixteen states and the District of Columbia are located in this area, and Gravatt (81) reports the disease occurs on *Acer* sp. in each of them. Gravatt's paper (81) is the most comprehensive that has yet appeared.

The disease has been reported causing serious damage to the box elder near Ottawa, Canada, by Drayton (65).

The syndromal characteristics in the main are essentially those displayed by other kinds of trees suffering from the disease. According to Rankin (160), Zimm (231), Colley (51), Gravatt (81), and others, the disease runs a rapid course generally ending in the death of the tree or part attacked. Old trees, forty years of age, are as severely affected as seedlings in the nursery. Similarly trees in high or low vigor are readily attacked. Rankin (160) states that after

becoming infected old or young trees may die in a few months' time. Colley (51) and Gravatt (81) state that when attacked, young trees may die within the year, while old trees succumb limb by limb until the entire tree is dead. In one instance Gravatt saw old, vigorously growing Norway maple trees killed within three years of the time they were attacked. Zimm, Colley, and Gravatt all regard the Norway maple as the most susceptible *Acer* species.

More resistant varieties may withstand the disease for years without serious injury, and even the susceptible varieties at times successfully withstand the attack for years without great injury. Gravatt assumes that strains of *Verticillium* of varying virulence exist, which accounts for the irregular behavior of the disease within individual varieties.

The infected sapwood becomes streaked with dark green discolorations (Gravatt, 81; Colley, 51; and Rankin, 160). Haenseler (89) describes this discoloration as bluish-black.

In addition to the usual characteristic symptoms of hadromycosis, the bark of certain maple species develops distinct cankers or lesions directly over the diseased wood which frequently emit a foul-smelling odor due to the fermenting sap. The lesions may appear simply as dark moist areas or streaks in the bark, but in very susceptible varieties such as the Norway maple, a typical slime flux may develop. Insects attracted to these diseased areas work further destruction to the trees. Subsequently the bark over the diseased areas dries out and falls off, leaving wounds resembling those made by lightning. Sugar and red maples are less apt to develop bark lesions, and thus far no one has reported them on either the sycamore maple or silver maple.

Van der Meer (193) has reported the disease in *A. platanoides* var. *schwedleri* Kock and has described briefly the bark lesions associated with it.

The cross-inoculation experiments and cultural studies of Zimm (231), Haenseler (89), Jagger and Stewart (110), and Bewley (24, 25, 28) are of interest. They have been discussed under "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

Bibliography.—Anonymous (2); Bewley (**24**, **25**, 28, 30); Colley (**51**); Drayton (65); Dufrenoy (72, 319); Gravatt (**81**); Haenseler (89, **94**); Hardesty (95); Jagger and Stewart (**110**); McCallum (322); Oppenheimer (134); Orton (136); Pape (140); Rankin (**160**); van der Lek (189); van der Meer (191, **193**); van Poeteren (198); Wollenweber (216, 218); Zimm (**231**). See also "Appendix" (p. 350).

Smoke Tree (*Cotinus coggygria* Scop.)

In 1924, Westerdijk and van Luijk (205) described a hadromycosis in this species and attributed it to *Verticillium albo-atrum.* No inoculation experiments were made. See "Sumac" (p. 310).

Van der Meer (191) lists this species in her host tables. No other reference to the disease in *Cotinus* sp. has appeared in the literature.

Sumac (*Rhus* sp.)

Smooth sumac.....*Rhus glabra* L.
Staghorn sumac.....*R. typhina* L.
Fragrant sumac.....*R. canadensis* Marsh.
Ill-scented sumac.....*R. canadensis* Marsh. var. *trilobata* (Nutt.) Gray.

In 1924, Westerdijk and van Luijk (205) described a hadromycosis in *Rhus glabra* L. and *R. typhina* L., also in *Cotinus coggygria* Scop. (*Rhus cotinus* L.), which they attributed to *Verticillium albo-atrum.* They made no inoculation tests but felt reasonably safe in concluding the disease to be due to its attack. In 1925, van der Meer (191, 192) also reported isolating a *Verticillium* from *Rhus typhina.* In 1927, Dufrenoy (70) referred to the disease in *Rhus canadensis* in America giving Barrus as reference.[36] In 1929 Dufrenoy (319) again very briefly referred to the disease in *R. canadensis.* In 1929, Gilman and Archer (320) reported *Rhus glabra* L., *R. typhina* L. and *Rhus canadensis* Marsh. var. *trilobata* (Nutt.) Gray as susceptible to attack by *Verticillium albo-atrum,* giving Melhus of the Iowa State Agricultural College at Ames, Iowa, as reference. Dr. Melhus apparently has never published a report on the disease in these three species.

The disease is severe in these species, the trees or bushes being easily killed by it. The syndromal characteristics as reported by Westerdijk and van Luijk (205) are essentially those of other woody plants having the disease.

No other writers have reported the disease in sumac.

Tapioca Plant (*Manihot utilissima* Pohl.)

See "Tobacco" (p. 311).

[36] Dr. Barrus, Cornell University, N. Y., has never published a report of the disease in this species. In a personal letter to me, however, he has confirmed Dr. Dufrenoy's report, which he had given to him personally.

Tobacco (*Nicotiana tabacum* L.)

In 1922, Averna-Saccá (10) published a short account of a disease of tobacco in Brazil which he attributed to *Verticillium albo-atrum* R. and B. From his description of it, the disease in no way resembles a hadromycosis, and accordingly, has no place in this paper. Of the disease he says:

> Tobacco in the seed beds is affected most, especially in low damp places or when excessively fertilized with horse manure that has been improperly cured.
>
> The young plants show on the upper parts, irregular spotting, at first scattered, later coalescing, livid, covered by a dense efflorescence of cotton-like aspect, whitish and finally ferruginous.
>
> In the leaves and rachis of the inflorescence the *Verticillium* displays the same characteristics. At times its growth fructifications are so intense it envelops and sticks the flowers together making them totally useless.
>
> In the seed beds the plants attacked by *Verticillium* are destroyed.

He recommends spraying with bordeaux mixture for the control of the disease.

He also simply reports finding the same fungus attacking potato tubers, kidney beans, banana trees, chayote plants, cacao trees, and tapioca plants in Brazil. Descriptions and experimental data are lacking.

In another paper (11) Averna-Saccá also reports the same fungus attacking coffee beans. (See "Coffee," p. 305.) A rather detailed description of the organism is given in this paper. From the descriptions given in these two papers it is rather doubtful whether the fungus isolated by Averna-Saccá is *Verticillium albo-atrum* R. and B. or its related forms associated with hadromycosis in various plants. Until more work is done with the disease in the several plants mentioned above, they should not be accepted unreservedly as hosts of *Verticillium albo-atrum* or related forms.

No other writers refer to the disease in tobacco, banana, chayote, tapioca plant, or kidney beans.

Tree of Heaven (*Ailanthus glandulosa* Desf.)

In 1929, Beach (326) isolated *Verticillium albo-atrum* from the wood and bark of several trees in a dying condition on the campus of the University of Pennsylvania. His report is very brief. No descriptions or experimental data are given. This is probably the first report of the disease in this plant.

BUSH FRUITS

Currant (*Ribes* spp.)

Northern red currant.....*Ribes rubrum* L.
European black currant.....*R. nigrum* L.

In 1907, Aderhold (1) reported a hadromycosis of currants and gooseberries due to a *Verticillium* sp. He regarded the disease as a thrombosis because of the obstructing mycelium in the vessels. Nursery stock was said to be severely affected. He was able to produce the disease in currants by inoculating the cut surfaces of stems which he placed in water.

In 1918, van der Lek (189) very briefly reported isolating a *Verticillium* from black currants affected with the disease in Holland. Descriptions and experimental data were not given.

Van der Meer (191, 192) reported the disease in the red currant varieties Hoornsche Roode and Fay's Prolific. She produced the disease in red currants by inoculating the branches with a pure culture of *Verticillium* from currant. She also isolated the organism from black currants and gooseberries.

Dufrenoy (72) briefly reported isolating the fungus from gooseberries in France.

The syndromal characteristics are essentially those observed in other plants affected with a *Verticillium* hadromycosis. In addition, a distinct edema or 'dropsy' not infrequently accompanies the disease. According to Aderhold (1), the affected trunks and branches swell to several times their natural size. Van der Meer (191, 192) reported the swelling to be confined to the portions of the trunk and branches invaded by the fungus. Thus the entire circumference of a stem may be involved or only a portion of it. The edema is due to the congestion of sap in the vessels. The cortex eventually ruptures and a watery exudate flows from the slits in the bark.

The wood of affected currant branches has "partially a bluish color" (van der Meer, 191).

Van der Meer (191) and Dufrenoy (72) refer to the organism as *Verticillium dahliae* Kleb. Aderhold (1) calls it *Verticillium* sp.

The disease has never been reported in America on currants and gooseberries.

Bibliography.—Aderhold (**1**); Berkeley and Jackson (21); Carpenter (49); Dufrenoy (72); van der Meer (**191**, **192**); van Poeteren (196).

Dewberry (*Rubus procumbens* Muhl. var. *roribaccus Bailey*), **BLACKBERRY** (*R. allegheniensis* Porter var. *sativus* Brainerd), and **Youngberry** (*Rubus* hybrid)

In 1923, I isolated a *Verticillium* sp. from Lucretia dewberry plants growing in a mixed berry patch near Palo Alto, California. Morphologically the organism was identical with the one which attacks a wide range of plants in California.

The syndromal characteristics were essentially the same as those observed in raspberries affected with the same disease, although the vivid purplish discoloration of the canes which ordinarily accompanies the disease in the latter was not observed in the several dewberry plants studied.

The owner of the patch later reported that he had observed identical symptoms in the Gardena dewberry, the Mammoth blackberry, the Cory thornless blackberry, and the red loganberry. In the absence of cultures and a suitable laboratory examination of material from these varieties, final proof of their susceptibility is lacking.

In 1927, Rudolph (257) reported the resistance of the red and black loganberry to the disease.

In 1912, Lawrence (117) briefly reported having isolated the fungus from the Snyder blackberry in Washington. In 1923, Shear (238) briefly reported bluestem in blackberries in Duchess County, New York. The disease was said to kill the bushes quickly. No experimental data were given. In 1924, an anonymous writer (239) reported the disease in blackberries in California. The disease was said to be severe in all berry regions of the state, particularly in San Mateo County. The losses were placed at 8 per cent. In 1925, an anonymous writer (240) reported the disease in blackberries in Minnesota. That same year, Rudolph (168) briefly mentioned the susceptibility of this species to the disease in California. These are the only references to the disease in blackberry that have appeared.

Youngberry plants observed near San Jose, California, have been seriously attacked by the disease. The fungus was isolated from affected canes by cultural methods.

Gooseberry (*Ribes grossularia* L.)

See "Currant" (p. 312).

Raspberry (*Rubus* spp.)

Red raspberry.....*Rubus idaeus* L.; *R. strigosus* Michx.
Black raspberry.....*R. occidentalis* L.

In 1912, Lawrence (117) described the disease in raspberries growing in Washington. He gave the name *Acrostalagmus caulophagus* to the organism. All varieties of black caps were considered susceptible, and he also isolated the same organism from the Red Antwerp raspberry and the Snyder blackberry.

In 1918, Carpenter (49) referred the organism to the genus *Verticillium* with the implication that it is specifically identical with, or at least closely related to *V. albo-atrum* R. and B. See "Identification of the Genus *Acrostalagmus* with *Verticillium*" (p. 205) for a discussion of relationship of *Verticillium* and *Acrostalagmus*. In 1923, Hockey (106) reported the disease in the Niagara district. He supported Carpenter's views, saying, "The organism differs very little from and probably is identical with *Verticillium albo-atrum Reinke and Berthold.*"

The disease has since been widely reported on the Pacific and Atlantic coasts of the United States. Also in Canada, particularly in the Niagara district. In 1923, the disease was first reported in the literature in California (42, 107), although it had been observed at a considerably earlier date.

In 1925, Harris (96) reported the disease in England on various red varieties. In 1926, Berkeley and Jackson (21) described *V. ovatum*, which they isolated from diseased red raspberry canes growing in the Niagara-Ontario district. In 1927, Karthaus (114) discribed the disease in red raspberries in Holland.

Characteristics of the Disease in Raspberries.—The syndromal characteristics of the disease in the leaves, canes, and roots are essentially the same as given under "Description of *Verticillium* Hadromycosis" (p. 210).

In addition to the slight blanching of the intervenal tissue of the leaf blades, the edges of the leaflets tend to curl upward from the margins exposing their undersides.

An intense purplish, or bluish-black discoloration of the canes ordinarily accompanies the disease. Even the petioles may develop this color. Under certain conditions, however, the discoloration may be wholly absent or so faint as to be indistinguishable from the color

developed normally by healthy, ripening canes. Similarly the discoloration may appear early in the course of the disease or not until long after infection has taken place. (Harris, 96, 98; Berkeley and Jackson, 20, 21; and author's observations.)

Not infrequently the discoloration on the cane first appears at a height of several inches above the ground rather than at or below ground level. This characteristic at first misled Lawrence (117) and caused him to think infection takes place above ground.

The discolorations may be observed first as an even and smoothly distributed area that encircles the entire cane at the base. In the young green shoots the discoloration presents a striking contrast to the green tissue, the line between the healthy and the diseased portions frequently being sharply drawn. The discoloration progresses up the stem at a variable rate according to climatic factors, the susceptibility of the variety, etc. Lawrence (117) measured the rate of spread in 42 shoots of Cumberland black raspberries and found it averaged 6.6 lineal inches a day. Under conditions favorable to the disease, a cane may be completely discolored a few days after the discoloration first appears. Figure 2 (p. 214) shows the characteristic discoloration developed on raspberry canes affected with the disease.

The affected wood shows the usual brown discoloration, and ordinarily the discoloration on the bark develops immediately over the diseased wood beneath. Since the disease may be confined to a mere strip in the total wood cylinder, the discoloration on the bark over it may appear as a sharply defined stripe.

The tendency of affected canes to develop a striped discoloration under the conditions in which he studied the disease, led Harris (96, 98) to recommend as a common name for the disease the term 'blue stripe wilt.' Lawrence (117), on the other hand, who observed both forms but found the type of discoloration which completely girdles the stem to prevail under the conditions in which he studied the disease, recommended the common term 'bluestem.' Berkeley and Jackson (21) prefer the simple term 'wilt' since the presence of discoloration on the canes is not an infallible proof of the presence of the disease. They base their use of the term on the leaf symptoms, which more closely approximate those of ordinary wilt due to lack of moisture than any other cause. This term leaves much to be desired also, since raspberry plants may also wilt from many causes, of physiological, fungus, and insect origin.

In California both the stripe and the girdling type of discoloration occur, the latter prevailing. In addition, under local conditions, the

discoloration not infrequently occurs as purplish blotches at the base of the petioles, particularly after the blades have been shed. Except for being stunted, the balance of the cane may present a normal appearance.

Discoloration of the canes is more pronounced in the black than in the red varieties (Berkeley and Jackson, 20, and author's observations).

The purplish color which becomes so pronounced on the canes at times is not a pigment. It is the result of an interplay of light on the normally pale grey-blue waxy bloom on the epidermis of the canes and the brownish-red to brownish-black discoloration that develops on the bark over the diseased wood of the cane. When the waxy bloom is rubbed away the brownish discolored bark is exposed, and the purple color disappears (Karthaus, 114; Lawrence, 117; and author's observations).

The presence of the disease in the canes may be suspected in the fall or early winter when the canes are stunted and show an abnormal purplish discoloration, also a poorly developed or shriveled condition of the buds.

In the spring the buds on the affected portions of the canes either fail to germinate or produce sickly, poorly developed shoots and leaves. Canes with dead buds upon them and poorly developed foliage present a ragged appearance. As the disease passes up the stem during the growing season the leaves are cast, the blade generally falling considerably in advance of the petiole. In the final stages of the disease a cane may be covered with bladeless petioles and surmounted by a tuft of poorly developed leaves which live for some time but eventually wither as the cane dies (fig. 2).

The fruit on affected canes not infrequently dries up before it matures. Fruit ripened on diseased canes is apt to be small, coarse, crumbly and woody, dry, tasteless, and of generally inferior quality (Lawrence, 117; Dodge and Wilcox, 61; Berkeley and Jackson, 20, 21; Karthaus, 114; Harris, 96, and author's observations).

In the roots the infected vessels of the xylem show the usual discoloration. At times the color may leach out of the vessels, staining all of the woody tissue a pronounced brownish-red.

Varietal Susceptibility.—Apparently there is no complete immunity to the disease to be found in raspberry varieties, but writers are universally agreed that the red varieties are more resistant than the black (Berkeley and Jackson, 20; Bennett, 16; Haenseler, 92; Lawrence, 117, and author's observations).

In the red varieties a mild infection may persist for years without destroying the patch for commercial purposes, but in black varieties the disease more often runs a short, fatal course. Berkeley and Jackson (20) point out that the black raspberries do not sucker, consequently a diseased plant is more apt to succumb than one of the red varieties which produces suckers. Suckers may be, and frequently are, wholly free of the disease. As the disease spreads in the roots, however, they may be attacked eventually and succumb with the plant. Red varieties, incidentally, do not sucker as plentifully when attacked by the disease (Harris 96, and author's observations). Harris found none of the red varieties with which he worked wholly resistant, although in some its effects were negligible.

Karthaus (114) observed that the red variety Superlative, growing immediately contiguous to the red variety Boskoop Hornet, showed remarkable resistance, whereas the Boskoop Hornet was seriously affected.

In California the disease is particularly destructive in the central coastal counties. The Ranere is widely grown, and it is probably the most susceptible of all red varieties. The black caps are not favored commercially and are not widely planted. They frequently are severely attacked by the disease.

One of the largest raspberry patches in the San Francisco Bay region was plowed up several years ago because *Verticillium* hadromycosis had rendered production unprofitable. The main planting was of the Ranere variety, although many other varieties were grown on a large scale. Cultures made from the canes of affected plants proved the identity of the disease. Under the existing conditions the Ranere and black caps suffered the worst of all. The Alton Improved seemed only slightly less susceptible; the Columbian Purple, Victory, and Cuthbert showed resistance in a distinct degree, although all were affected by the disease. The most resistant of all was the Syracuse, but it was not immune.

In various patches in the San Francisco Bay region the Cuthbert has generally shown somewhat greater resistance to the disease than the Ranere.

Harris (96) claims that while almost identical taxonomically with Red Antwerp A, a very susceptible variety, the Black Antwerp A was the most resistant of the several varieties he worked with.

The following red varieties are susceptible to the disease:

Ranere (St. Regis) (20, 21, 22, 42, 106, 167, 168); Cuthbert (16, 19, 20, 21, 22); Red Antwerp (96, 117); Antwerp Red A, Antwerp

Red B, Antwerp Black A, Baumforth's Seedling A, Reader's Perfection, Prior's Prolific, Mitchell's Seedlings (96, 100); Baumforth's Seedling (15); Baumforth's Seedling B, Lloyd George (96, 98); Viking (20, 21, 22); Herbert (20, 21); Boskoop Hornet (114); Marlborough (Bath's Perfection) (15, 20, 21, 22, 96, 98, 100); Syracuse, Alton Improved, Columbian Purple, Victory (author's observations).

The following black varieties are susceptible to the disease: Cumberland (16, 20, 92, 117, 323); Plum Farmer (20, 230); Mungers (230); Gregg (20); Parker (117).

Losses Due to the Disease.—In California, particularly in the San Francisco Bay region, the losses frequently are very heavy. The disease varies from a negligible amount in some patches to epidemic proportions in others. Already a number of patches which were once highly remunerative have been plowed up because of the disease. Such losses must be regarded as 100 per cent.

Lawrence (117) describes commercial patches of black raspberries in which every plant was affected. Bennett (16) has described a patch of Cumberland black raspberries in Michigan in which 50 per cent of the plants were killed in three years and another patch which was taken up one year after planting because of the inroads made by the disease. Losses in the Plum Farmer black raspberry amounting to 52 per cent have been reported by Zeller (230). In one field which he examined most of the plants were dead or dying one year after planting.

In Canada, Berkeley and Jackson (19) and Drayton (65, 66) report that in 1924 three-fourths of the Cuthbert plantations showed the disease, the average amount of infection in each amounting to 10 per cent. Berkeley and Jackson (20, 21) report infection in black caps as high as 40 per cent, and in red varieties (Cuthbert), 20 per cent. In certain cases every plant in the patch was attacked by the disease.

Species of Verticillium Reported Causing the Disease in Raspberries.—The following species of *Verticillium* have been described on raspberries suffering from hadromycosis: *Acrostalagmus caulophagus* by Lawrence (117); *Verticillium albo-atrum* by Carpenter (49), Hockey (106), Rudolph (167), Dodge and Wilcox (61), and Zeller (230); *Verticillium dahliae* by Karthaus (114), and Wormald (228); and *Verticillium ovatum* by Berkeley and Jackson (21), and Bennett (16). See "Discussion of *Verticillium* Species Associated with Hadromycosis" (p. 244).

Bibliography.—Ann. Rept. Univ. Calif. (42); Beaumont (316); Beaumont and Hodson (15); Bennett (16); Berkeley (18); Berkeley and Jackson (19, **20**, **21**, 22); Boyer (35); Butterfield (41); Carpenter (49); Dodge and Wilcox (61); Drayton (65, 66, 318); Dufrenoy (72, 319); Giddings (323); Haenseler (92); Harris (**96**, **97**, 98, 100); Hockey (**105**, 106); Horne, Essig, and Herms (107); Karthaus (**114**); Lawrence (**117**); Rankin (161, 162, 163); Rudolph (**167**, 168); van der Meer (191); Wormald (221, 222, 223, 224, 228); Zeller (230); Zundel (233). See also "Appendix" (p. 350).

ORNAMENTALS, FLOWERING PLANTS, SHRUBS, AND WEEDS

American Spikenard (*Aralia racemosa* L.)

In 1925, Chupp (309) very briefly attributed "wilt" of American spikenard to *Verticillium* sp. In 1927, Dufrenoy (70) reported having isolated *V. dahliae* from this plant while in the United States. In 1929 he reported the disease again (319).

Experimental data and descriptions of the disease in this species are wholly lacking. No other reference to the disease in this species has appeared in the literature.

Arbor-Vitae (*Thuja* sp.)

In his paper discussing wilt diseases due to *Verticillium alboatrum* R. and B., van der Lek (189) says in a footnote to his host table, "In 1915 Mr. Schoevers grew a *Verticillium* sp. from dying grafts of *Thuja* from Boskoop." Other than this brief report, no reference has been found in the literature to the disease in this species. Schoevers apparently never published a report of his work. Whether *Thuja* sp. is actually subject to *Verticillium* hadromycosis cannot be concluded definitely from the limited information at hand.

Aster (*Aster* spp.)

Italian aster	*Aster amellus* L.
Common blue wood aster	*A. cordifolius* L.
Calico aster	*A. diffusus* Ait.
White heath aster	*A. ericoides* L.
New England aster	*A. novae-angliae* L.
New York aster	*A. novi-belgii* L.
Panicled aster	*A. paniculatus* Lam.
Michaelmas daisy	*A. tradescantii* L.
Small white aster	*A. vimineus* Lam.

In 1920, Wiltshire (210) described the disease in aster (Michaelmas daisy). He isolated a fungus, which he did not name, from the diseased vessels. No inoculations were made to prove the pathogenicity of the organism.

In 1922, Dowson (62, 63) studied the disease and produced it in healthy plants by inoculating them with a fungus from diseased Michaelmas daisy plants. He referred the organism to the genus *Cephalosporium.* In 1923, Dowson (64) further described the disease, and gave a technical description of the fungus which he named *Cephalosporium asteris.* His studies of the morbid physiology of plants affected with the disease are of interest. See page 227. In 1924, Westerdijk and van Luijk (205) published the results of their studies of the fungus, cultures of which they had obtained from Dowson. They referred it to the genus *Verticillium.*

The syndromal characteristics are the same as those developed in other varieties affected with *Verticillium* hadromycosis. As in bush fruits, the suckers coming up from the roots may or may not become infected. Plants of susceptible varieties are frequently entirely killed. The leaves, before completely drying up and turning brown, are said to develop a bright lemon yellow color as the disease advances up the stems.

Varietal resistance varies considerably with the species of *Aster.* Members of *A. novi-belgii* are said to be particularly susceptible, while those of *A. novae-angliae* show a certain degree of resistance (Dowson 64).

Dowson (63, 64) reports that the disease occurs naturally in, or may be produced artificially by inoculating the following species: *Aster novi-belgii* L., *A. novae-angliae* L., *A. amellus* L., *A. cordifolius* L., *A. ericoides* L., *A. vimineus* Lam., *A. diffusus* Ait., *A. paniculatus* Lam.

The following varieties are specifically mentioned: Climax, Mrs. S. A. de Graaf, Avalanche, Mons, Empress, Anita Ballard, Ada, Gladys Donellan, Malines, Magnet, Saturn, Heather Glow. The Climax is particularly susceptible.

According to *The Plant Disease Reporter Supplement* (268), Gram and Rostrup (80) report *Verticillium vilmorinii* on *Aster tradescantii,* in Denmark.

The disease has never been reported in *Aster sp.* in America.

Bibliography.—Dufrenoy (72); Dowson (**62**, **63**, **64**); Gram and Rostrup (80); Westerdijk and van Luijk (205); Wiltshire (**210**, 211). See also "Appendix" (p. 350).

Barberry (*Berberis thunbergii* D. C.)

In 1918, Jagger and Stewart (110) reported the disease in *Berberis thunbergii* D. C. These writers isolated a *Verticillium* sp. from affected plants and produced the disease in healthy plants by inoculating them with it. Their cultural studies are of interest.

Very shortly after Jagger and Stewart's paper appeared, Zimm (231) published the abstract of a paper read before the American Phytopathological Society in which he also reported the disease in barberry and gave the results of his cultural studies.

'Blight' of Japanese barberry has been attributed to *Verticillium* sp. (237). Whether this disease is a true hadromycosis is not clear. Some experiments with barberry are reported under "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

The syndrome as described by Jagger and Stewart (110) is essentially that observed in other woody plants affected with the disease.

Bibliography.—Berkeley and Jackson (21); Gravatt (81); Haenseler (89); Hardesty (95); Jagger and Stewart (**110**); van der Lek (189); Wollenweber (216); Zimm (**231**).

Black Nightshade (*Solanum nigrum* L.)

See "Poppy" (p. 330).

Boston Ivy (*Parthenocissus tricuspidata* Planch. var. *veitchii* Rehd.)

In 1918, van der Lek (189) very briefly reported isolating a *Verticillium* from the discolored wood of "*Ampelopsis veitchii* Hort." (*Parthenocissus tricuspidata* var. *veitchii* Rehd.) in Holland. A satisfactory description of the disease in this plant is lacking. Experiments to prove the pathogenicity of the fungus were not made. Van der Meer (191) includes "*Ampelopsis veitchii*" in her table of plants subject to *Verticillium* hadromycosis. No other reference to the disease in this plant has been found.

Box (*Buxus sempervirens* L.)[37]

In 1925, Gravatt (81) reported the disease in box without giving descriptions or experimental data. No other writer has reported the disease in this species.

Bur Clover (*Medicago hispida* Gaertn.)

In 1926, I succeeded in infecting healthy young plants of bur clover. The plants were carefully lifted and largely shaken free of

[37] The specific name of *Buxus* confirmed by Gravatt in a letter.

adhering soil and replanted in a pot of soil which had been copiously mixed with *Verticillium* from different sources, namely, raspberry, tomato, and apricot plants, and growing in pure culture on Czapeck's synthetic nutrient agar. The clover developed a dull unhealthy color and remained stunted, which may have been due to the disease or to the conditions under which it was growing. Plantings were made from numerous stems above ground and in three instances *Verticillium* sp. developed in pure culture on Czapeck's synthetic nutrient agar.

Except for a brief previous report of the susceptibility of bur clover to attack by *Verticillium* which was made in 1926 (168), no reference to the disease in this common weed has appeared.

China Aster (*Callistephus chinensis* [L.] Nees.)

In 1906, Guéguen (82) first described the disease in the China aster (Reine-marguerite). Undecided at first whether the fungus, which he isolated from diseased specimens presented to him by Dr. de Vilmorin, should be classified as a new species of *Acrostalagmus* or *Verticillium,* he finally named it *Acrostalagmus vilmorinii.* Guéguen did not establish the pathogenicity of this fungus experimentally.

In 1918, Carpenter (49) upon the basis of Guéguen's elaborate descriptions of the fungus, referred it to the genus *Verticillium* with the statement that it is either identical with or very closely related to *V. albo-atrum.*

In 1925, van der Meer (191, 192) again reported the disease in the China asters under the old name *Aster chinensis* L.

The disease has never been reported in China asters in America.

In addition to the usual symptoms characteristic of a *Verticillium* hadromycosis, Guéguen (82) states that the bark over the affected area of the stems of China asters is easily decorticated.

Bibliography.—Carpenter (49); Guéguen (**82**); van der Lek (189); van der Meer (**191**, **192**).

Chrysanthemum (*Chrysanthemum* spp.)

Ox-eye daisy .....Chrysanthemum leucanthemum L.
Italian chrysanthemum.....Chrysanthemum indicum Cass.

In 1924, Haenseler (89) included *Chrysanthemum* in a list of plants subject to *Verticillium* hadromycosis in New Jersey.[38] Since then the disease has been reported in that state on several occasions. Haenseler (241) inoculated chrysanthemum plants with *Verticillium*

[38] The authorship of this unsigned paper was acknowledged in a personal letter.

albo-atrum and produced the disease. He reports observing the disease in thirteen varieties of chrysanthemum growing in the open and in greenhouses. The only varieties mentioned are the Pink Seilwich, Early Snow, and P. A. Dove, which are said to be very susceptible.

Nelson (242) reported the disease on *Chrysanthemum* in Michigan. In 1925, van der Meer (191, 192) reported the disease in *Chrysanthemum indicum* Cass. and *C. leucanthemum* L. in Holland. She referred the causal organism to *Verticillium dahliae* Kleb. Dufrenoy (72) includes these two species of *Chrysanthemum* in his host table.

Suitable descriptions of the disease in *Chrysanthemum* and experimental data are lacking.

Bibliography.—Dufrenoy (72); Haenseler (89, 93, 241); Martin (123, 124); Nelson (242); Rutherford (242); van der Meer (**191**, **192**); White (324). See "Appendix" (p. 350).

Cineraria (*Senecio cruentus* D. C.)

In 1928, White (325) very briefly reported *Verticillium* wilt of cineraria plants at Clinton, New Jersey. Descriptions and experimental data are wholly lacking. This is probably the only reference to the disease in *Cineraria* that has appeared.

Cockle Bur (*Xanthium* sp.)[39]

See "Velvet Leaf" (p. 334).

Common Mallow Weed (*Malva rotundifolia* L.)

In 1925, I succeeded in infecting healthy mallow weed plants with *Verticillium* isolated from diseased raspberry and tomato plants. The mallow plants were lifted while small and the roots shaken free of adhering soil. Stab wounds were made low in the tap root, and inoculations were made. The inoculum consisted of masses of spores, mycelium, and sclerotia scraped from the surface of pure cultures of the fungus on Czapeck's synthetic nutrient agar. Three plants were inoculated with *Verticillium* from tomato, and three with *Verticillium* from raspberry. Controls were prepared; three mallow plants were wounded as before, but no inoculum was introduced into the wounds. The plants were replanted in pots, one plant to a pot.

All three plants inoculated with the *Verticillium* from tomato, and one plant with *Verticillium* from raspberry contracted the disease. The fungus was recovered from the tap roots high above the point of original inoculation.

[39] In a personal letter, Dr. Haenseler has identified *Xanthium* sp. as cockle bur.

The syndromal characteristics were essentially those observed in other plants affected with the disease. The control plants had attained a size twice as large as the sick plants at the time the experiment was concluded.

Except for a mere reference to the disease in mallow weeds which was made in a popular article published in 1926 (168), no report of the disease in this species has appeared.

Dahlia (*Dahlia variabilis* Desf.)

In 1913, Klebahn (113) described the disease in plants of the Gieselher variety suffering from an autochthonous infection. He isolated a species of *Verticillium* from the affected tissues and called it *V. dahliae*. See "The Relation Between *Verticillium albo-atrum* R. and B. and *V. dahliae* Kleb. (p. 247).

Klebahn (113) proved the pathogenicity of his fungus with suitable inoculation experiments. In certain cases he inoculated the tubers with the fungus before planting, and in other experiments he planted healthy tubers in pots of soil to which pure cultures of the fungus had been added. He used twelve varieties of dahlia, but the inoculations were successful only in the Gieselher.

The syndromal characteristics are essentially the same as those developed by other plants affected with *Verticillium* hadromycosis. As in the case of potato tubers the dahlia roots or tubers show a brownish discoloration in the tissue, and the disease is probably easily disseminated through the use of such infected stock for seed.

Klebahn seems to be the only one to have worked with the disease in dahlia with the exception of van der Meer (191, 192), although a number of workers refer to Klebahn's paper.

Bibliography.—Berkeley and Jackson (21); Carpenter (47, 49); Dufrenoy (68, 72, 319); Haenseler (89); Jagger and Stewart (110); Klebahn (**113**); Orton (136); van der Lek (188, 190); van der Meer (**191**, 192); Wollenweber (216).

Dandelion (*Taraxacum officinale* Weber)

In 1926, I succeeded in infecting several mature, healthy dandelion plants possessing large tap roots with a *Verticillium* sp. isolated from diseased raspberries.

The plants were carefully lifted, inoculated by means of a stab wound in the tap root into which was introduced sclerotia and spores scraped from the surface of a pure culture of the fungus growing on

Czapeck's synthetic nutrient agar, and replanted in pots. Controls were similarly treated except that no inoculum was used.

The outer leaves of infected plants died first, the youngest leaves in the center of the whorl being the last to succumb. In the final stages, only poorly developed blossoms remained alive in the center of a dead whorl of leaves. The woody tissue in the tap roots of such plants was streaked a deep reddish-brown and was noticeably water-soaked or edematous. The fungus was recovered from such tissue taken high above the point of original inoculation. The controls remained healthy and grew normally.

Except for a mere reference to the susceptibility of this weed to attack by *Verticillium* which was made in 1926 (168), no reference to the disease in this plant has appeared.

Daphne (*Daphne mezereum* L.)
See "Poppy" (p. 330).

European Mallow (*Malva alcea* L.)
See "Poppy" (p. 330).

Flea-Bane (*Erigeron canadensis* L.)
See "Poppy" (p. 330).

Dufrenoy (72) referring to van der Meer, lists this plant in his host table.

Flowering Peach (*Prunus persica* Sieb. and Zucc.)

For the past three years a large, mature tree, over 20 feet in height, of the double-flowered, pink variety of ornamental or flowering peach in the grounds of the University of California Deciduous Fruit Field Station at San Jose, has been affected with *Verticillium* hadromycosis. Last year a limb over 3 inches in diameter died, but other large limbs affected at the time survived and do not show the outward symptoms of the disease this year. Wood hitherto unaffected shows the disease, however.

The syndromal characteristics are identical with those seen in commercial fruit-producing varieties attacked by the disease.

Cultures were made from the affected wood, and the organism found to be the *Verticillium* which attacks widely unrelated plants in California. No inoculation studies have been made.

It is believed this report of the disease in the flowering or ornamental peach is the first that has appeared. See "Peach" (p. 303).

Goosefoot (*Chenopodium album* L.)

See "Poppy" (p. 330).

Ground Cherry (*Physalis alkekengi* L.)

In 1922, Wollenweber (216) included *Physalis alkekengi* in his list of plants subject to wilt by *Verticillium albo-atrum* R. and B. Neither descriptions nor experimental data relating to the disease in this variety accompany his report. Van der Meer (191) and Dufrenoy (72) referring to Wollenweber's paper, include this species in their host tables. No other writers mention the disease in *Physalis* sp. It has never been reported in America in this plant.

Groundsel (*Senecio vulgaris* L.)

In 1925, van der Meer (191, 192) first reported the disease in this weed plant in Holland. See "Poppy" (p. 330).

Dufrenoy (72) referring to van der Meer's paper, lists this plant in his host table.

In 1925, I succeeded in infecting young seedlings of this common weed with *Verticillium* from raspberry and apricot plants. The young plants were lifted and the roots shaken free of the adhering soil. They were then replanted in pots to which had been added pure cultures of the fungus growing on Czapeck's synthetic nutrient agar. *Verticillium* from only one source was used in any one pot. Controls were provided but no inoculum was added to the soil.

In general the syndromal characteristics were those of a typical *Verticillium* hadromycosis.

The fungus was recovered from the main stem of numerous plants which had become infected with the *Verticillium* from the two original sources mentioned above.

This is probably the first reference to the disease in groundsel in America.

Heliotrope (*Heliotropium* sp.)

In 1928, Bryan (39) briefly reported an autochthonous infection of heliotrope plants growing in the grounds of the Department of Agriculture at Washington, D. C. She isolated a species of *Verticillium* resembling *Verticillium albo-atrum* and succeeded in infecting healthy potted plants with it. The syndromal characteristics apparently are much the same as those displayed by other plants affected with *Verticillium* hadromycosis. No other writer has reported the disease in heliotrope.

Horse Nettle (*Solanum carolinense* L.)

In 1918, Jagger and Stewart (110) reported an autochthonous infection of *Solanum carolinense* L., *S. rostratum* Dunal., *S. integrifolium* Poir., *S. torvum* (wild eggplant from Porto Rico), *S. eleagnifolium* Cav., *S. marginatum* L., and *S. pyracanthum* Jacq. planted experimentally in a field in which eggplants had been attacked severely with *Verticillium* hadromycosis. Descriptions of the disease in these varieties are not given but the authors say, "Many of these developed the characteristic symptoms of the disease, and a large number of isolations were made, the characteristic *Verticillium* fungus of eggplants being obtained. . . . . "

Haenseler (93) reports the horse nettle to be especially susceptible to attack. Van der Lek (189) and van der Meer (191) list these plants in their host tables, citing Jagger and Stewart as reference, as does Dufrenoy (70) for *Solanum pimpinellifolium* Dunal. No other writers have reported the disease in these species.

Bibliography.—(*Solanum carolinense* L.) Haenseler (89, 93); Jagger and Stewart (110); van der Lek (189); van der Meer (191).

Japanese Pittosporum (*Pittosporum tobira* Ait.)

In 1928, Professor J. McMurphy of Leland Stanford Jr. University, California, isolated a fungus from this ornamental which he referred to *Verticillium albo-atrum*. The tips of young shoots on more than half of a large plant on the University campus were wilted. Twenty-five plantings from diseased wood gave eighteen apparently pure cultures of *Verticillium* which produced conidiophores and minute sclerotia. Cuttings taken from the seemingly healthy parts of the plant rooted and grew well. They show no symptoms of disease at the present time. The syndromal characteristics of the disease are essentially the same as observed in other plants affected with the disease.

This is the first report of the disease in *Pittosporum* to appear, and it is included in this paper with the permission of Professor McMurphy.

Lilac (*Syringa vulgaris* L.)

In 1922, van Poeteren (195) briefly described a disease of lilacs in a nursery at Naarden, Holland, which from his description was probably a *Verticillium* hadromycosis. In one instance *Verticillium* was isolated from an affected plant. The author withheld final opinion as to the etiology of the disease pending further experimentation.

In 1925, van der Meer (191) conclusively proved the lilac to be susceptible. Experimentally she produced the disease in healthy lilac plants by inoculating them with *Verticillium* from diseased lilac. Further descriptions of the disease were given. Both the white and colored-flower varieties are attacked.

The syndrome is essentially that observed in other plants affected with *Verticillium* hadromycosis. In addition to the more characteristic symptoms, namely, stunting of the plants, discoloration of the wood vessels, and desiccation of the foliage, van der Meer (191) reports the leaf parts of affected blue lilacs assume a purplish color.

The disease has never been reported in lilacs in America.

Bibliography.—Berkeley and Jackson (21); Dufrenoy (72); Gravatt (81); Pape (140); van der Meer (**191**, **192**); van Poeteren (**195**).

Lombart's Flowering Currant (*Ribes sanguinium* Pursh. var. *lombartii*)

See "Poppy" (p. 330).

Lupine (*Lupinus* sp.)

Many-leaved Lupine.....*Lupinus polyphyllus* Lindl.

In 1922, Wollenweber (216) very briefly reported a wilt of lupines due to a *Verticillium* to which he gave the name *Verticillium angustum* Wollenweber. See "The Relation of *Verticillium albo-atrum* R. and B. to Other *Verticillium* Species Known to Produce Hadromycosis in Plants" (p. 252) for further discussion of this species. Neither descriptions nor experimental data relative to the disease in lupine accompanies his report.

In 1925, van der Meer (191, 192) reported the disease in *Lupinus polyphyllus* Lindl. in Holland and attributed it to *Verticillium dahliae Kleb.* Her inoculations of *L. polyphyllus* with *Verticillum* from diseased plants of this same species were unsuccessful, but she succeeded in infecting healthy plants with *Verticillium* from various other hosts. In 1927, Pape (140) briefly described the disease in lupines.

The disease has never been reported in lupines in America.

Bibliography.—Pape (**140**); Utkin (186); van der Meer (**191**, **192**); Wollenweber (216).

Maltese Cross (*Lychnis chalcedonica* L.)

Van der Lek (189) includes this ornamental in his list of plants subject to attack by *Verticillium albo-atrum* R. and B. in Holland. No descriptions or experimental data are given. No other reference to the disease in this plant has been found.

Mint (*Mentha* sp.)

In 1926, Nelson (267) reported a wilt of peppermint plants which had been under observation for two years in the vicinity of Kalamazoo, Michigan. On one farm the disease had occasioned heavy losses. Apparently Nelson was not absolutely sure about the etiology of the disease, since he attributes it to *Verticillium* sp. and places a question mark after the name of the fungus. Dufrenoy (72) includes *Mentha* sp. in his host table giving Nelson as reference. No other writers have reported the disease in *Mentha*.

Nettle (*Urtica urens* L.)

See "Poppy" (p. 330).

Oswego Tea (*Monarda didyma* L.)

See "Poppy" (p. 330).

Pearly Everlasting Flower (*Gnaphalium margaritaceum* L.)

See "Poppy" (p. 330).

Dufrenoy (72) referring to van der Meer, lists this plant in his host table.

Peony (*Paeonia* sp.)

In 1927, Hardesty (95) briefly described the disease in peony plants. Dufrenoy (70, 319) also has isolated the fungus from plants growing in New York State. White (279, 280) has reported the disease in Kansas. A suitable description of the disease in this species and experimental data covering proof of the pathogenicity of the fungus are lacking. No other writers refer to the disease in peony.

Phlox (*Phlox* spp.)

Annual phlox.....*Phlox drummondii* Hook.
Summer perennial phlox.....*P. decussata* Hort.

Van der Meer (191, 192) succeeded in infecting healthy *Phlox decussata* plants with *Verticillium* isolated from diseased plants of

the same species. She also isolated the fungus from *Phlox drummondii* affected with the disease.

See also "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235), and "Poppy" (p. 330).

Pink (*Dianthus* sp.)

In 1927, Dufrenoy (72) included *Dianthus* in his list of plants susceptible to *Verticillium* hadromycosis. In 1928 (71), he reported isolating the fungus from the pink growing at the Antibes School of Agriculture. The syndromal characteristics apparently are the same observed in other plants which have contracted the disease. No other writers have reported the disease in *Dianthus,* although several include this genus in their host tables giving Dufrenoy as reference.

Poppy (*Papaver* spp., *Eschscholtzia* sp.)

Shirley and corn poppy.....*Papaver rhoeas* L.
Oriental poppy.....*P. orientale* L.
California poppy.....*Eschscholtzia californica* Cham.

In 1925, van der Meer (191, 192) reported having isolated *Verticillium dahliae* from these three species of poppy suffering from hadromycosis. Among other new hosts mentioned by her in the same papers are *Phlox drummondii* Hook; *Phlox decussata* Hort., *Aconitum napellus* L., *Monarda didyma* L., *Campanula macrantha* Fisch., *Gnaphalium margaritaceum* L., *Ribes sanguineum* Pursh. var. *lombartii., Daphne mezereum* L., *Sambucus racemosa* L., *Urtica urens* L., *Erigeron canadensis* L., *Senecio vulgaris* L., *Chenopodium album* L., and *Solanum nigrum* L.

Van der Meer has not given individual descriptions of the disease in these new hosts, but in her paper she has given a general description of *Verticillium* hadromycosis which is essentially the same as that given under "Description of *Verticillium* Hadromycosis" (p. 210) of this paper. It may be inferred, therefore, that the syndromal characteristics of the disease in the above-mentioned hosts are essentially the same as those occurring in other plants attacked by the disease.

Van der Meer has referred to the *Verticillium* which she isolated from these hosts as *V. dahliae* Kleb. See "The Relation Between *Verticillium albo-atrum* R. and B. and *V. dahliae* Kleb. (p. 247) for a further discussion of this species. She conducted extensive inoculation experiments with the fungus isolated from these plants to prove the pathogenicity of the organism.

No other writer has reported the disease in these species.

In 1925 I succeeded in infecting young Shirley poppy (*Papaver rhoeas* L.) and California poppy plants (*Eschscholtzia californica* Cham.) with the *Verticillium* sp. which attacks a wide range of plants in California. Young vigorous plants, not more than 6 inches in height, were lifted shortly after they had appeared above ground. The adhering soil was largely shaken away from the roots, and the plants were densely replanted in pots of soil to which had been added, in copious amounts, a mixture of pure cultures of *Verticillium* from apricot, raspberry, and tomato plants growing on Czapeck's synthetic nutrient medium. Controls were prepared in the same way, but the soil was not inoculated with the fungus.

The infected plants remained stunted and developed a sickly appearance which in a general way resembled a typical *Verticillium* hadromycosis. The organism was recovered by cultural methods from the main root and stems of the affected plants.

In another experiment several mature *Eschscholtzia californica* plants were inoculated with *Verticillium* from raspberry. The plants were lifted and a stab wound made low in the main root of each into which sclerotia and spores scraped from a pure culture of the fungus growing on Czapeck's synthetic nutrient medium were introduced. The plants were then replanted in pots. Several plants were wounded in a similar manner for controls. No inoculum was used. The infected plants ceased to thrive and died slowly. The vascular system in the main root of each was discolored deep brown. The controls remained perfectly healthy. The fungus was recovered by cultural methods from tissue taken from the main root high above the point of inoculation.

Red-Berried Elder (*Sambucus racemosa* L.)

See "Poppy" (p. 330).

Dufrenoy (72) referring to van der Meer, lists this plant in his host table.

Rose (*Rosa* sp.)

In 1924, Haenseler (89)[40] included rose in his list of plants subject to *Verticillium* hadromycosis in New Jersey. Other writers who have included rose in host tables are Martin (124) and Gravatt (81). Descriptions and experimental data covering the disease in this plant are wholly lacking.

In 1926, I isolated *Verticillium* sp. from a dying rose bush, of the Belle of Portugal variety, taken from the grounds of the State Capitol

[40] The authorship of this unsigned paper acknowledged in a personal letter.

at Sacramento, California. The fungus was identical culturally and morphologically with the *Verticillium* associated with hadromycosis in a wide range of plants in California.

The syndromal characteristics of the disease were essentially the same as those observed in other plants suffering from a *Verticillium* hadromycosis. In addition to the characteristic brown-streaking of the sap wood, the epidermis was discolored a pronounced brown in sharply defined stripes which lay immediately over the region of the stem inhabited by the fungus. Inoculation tests were not made.

Rough Pigweed (*Amaranthus retroflexus* L.)

In 1925, I isolated a *Verticillium* sp. from this common weed growing near the University of California Deciduous Fruit Field Station. The fungus was obtained in pure culture from the roots and main stem at many points above the ground and was identical morphologically and culturally with the *Verticillium* isolated from a wide variety of plants in California.

The plant from which cultures of the fungus were obtained was one of a great many showing similar symptoms and was growing in an apricot orchard which was interplanted with tomatoes. Both the tomato plants and apricot trees were suffering from an attack of *Verticillium* hadromycosis of unusual severity. Many scattered plants of pigweed growing in the orchard appeared normal and attained a height of 3 to 4 feet. Others remained stunted and sickly, and in general displayed symptoms of a typical *Verticillium* hadromycosis. The flower heads drooped, and the leaves hung more or less limp from the branches.

Except for a mere reference to the susceptibility of this plant to the disease which was made in 1926 (168), no reference to the disease in this common weed has appeared.

Royal Bellflower (*Campanula macrantha* Fisch.)
See "Poppy" (p. 330).

Dufrenoy (72) referring to van der Meer's paper, lists this plant in his host table.

Sand Bur (*Solanum rostratum* Dunal.)
See "Horse Nettle" (p. 327).

Scarlet Eggplant (*Solanum integrifolium* Poir.)
See "Horse Nettle" (p. 327).

Silver-Leafed Nightshade (*Solanum eleagnifolium* Cav.)

See "Horse Nettle" (p. 327).

Snapdragon (*Antirrhinum* sp.)

Common snapdragon.....*Antirrhinum majus* L.

In 1914, Brown (37) briefly reported the disease in snapdragons growing in the gardens and greenhouses of the United States Department of Agriculture at Washington, D. C.. She isolated a *Verticillium* sp., which Carpenter (49) identified as *V. albo-atrum*, and successfully produced the disease in healthy plants by inoculating them with it.

In 1921, Bewley (24) infected snapdragons with *Verticillium* from tomato. Carpenter (49) also reports cross-inoculation experiments. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

In 1925, van der Meer (191, 192) reported the disease in *Antirrhinum majus* L. in Holland.

The syndrome has not been fully described by the writers who have reported the disease in this plant. Presumably the characteristic symptoms of a *Verticillium* hadromycosis are developed.

Bibliography.—Berkeley and Jackson (21); Bewley (**24**, **25**, 26, **28**, 30); Brown (**37**); Carpenter (47, **49**); Dufrenoy (72); Haenseler (89); Jagger and Stewart (110); Pethybridge (153); van der Lek (189); van der Meer (**191**, **192**); Weimer (203); Wollenweber (216). See also "Appendix" (p. 350).

Solanum marginatum L.

See "Horse Nettle" (p. 327).

Solanum pyracanthum Jacq.

See "Horse Nettle" (p. 327).

Sweet Pea (*Lathyrus odoratus* L.)

In 1922, Bewley (25) briefly reported the disease in sweet peas. The plants were affected when 6 inches tall. The syndrome is essentially the same as observed in other plants affected with *Verticillium* hadromycosis. *V. albo-atrum* R. and B. was isolated from the diseased plants and the disease produced in healthy plants by inoculating them with it. Details of the experiments were not given. See also "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235).

The disease has never been reported in sweet peas in America.

Bibliography.—Bewley (**25**, 26, 28, 30); Dufrenoy (68, 72); van der Meer (191).

True Monkshood (*Aconitum napellus* L.)

Van der Meer (191, 192) inoculated healthy plants of *Aconitum napellus* with *Verticillium* from diseased plants of the same species, with doubtful results. She succeeded in infecting plants of this species with *Verticillium* isolated from several other host plants, however. See "Cross-Inoculation Experiments with *Verticillium* Species" (p. 235), and "Poppy" (p. 330).

Velvet Leaf (*Abutilon theophrasti* Medic.)

In 1914, Carpenter (47) very briefly reported and described the disease in two weeds in New Jersey, namely, *Abutilon* and *Xanthium* spp. Outside of mentioning the discoloration of the vascular system of these plants no further symptoms were discussed. Haenseler (89) referring to other workers, also has reported the disease in *Abutilon* and *Xanthium* spp. in New Jersey.

Bibliography.—(*Abutilon* and *Xanthium* spp.) Carpenter (**47**, 49); Dufrenoy (72); Haenseler (89); Jagger and Stewart (110); van der Lek (189, 190); van der Meer (191).

Veronica (*Veronica elliptica* Forst.)

In 1924, Professor J. McMurphy of Leland Stanford Jr. University, California, personally described the disease in *Veronica* to me. He had isolated *Verticillium* from the wood of affected plants. He assigned the problem to a student who did considerable work with the disease in *Veronica* but who left the University without publishing the results of his experiments. With the permission of Professor McMurphy I am including this genus in the list of plants subject to *Verticillium* hadromycosis. The syndromal characteristics are essentially the same as observed in other plants attacked by the disease. No other report of the disease in *Veronica* has appeared.

Wild Florida Eggplant (*Solanum floridanum Shuttlew.*)

In 1927, Haenseler (253) very briefly reported this species to be too susceptible to the disease to be of value in breeding for resistance. No experimental data or descriptions were given. No other writer has reported *Verticillium* hadromycosis in this species.

Wild Porto Rico Eggplant (*Solanum torvum* Sw.)

See "Horse Nettle" (p. 327).

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APPENDIX

Brief reports of the disease have appeared from time to time in the *Plant Disease Reporter*.[42] These reports frequently are unsigned, and it has been found more convenient to list them under the individual plants considered rather than under the names of the authors.

ALMOND

234. Pl. Dis. Rep. Sup. 33:113, 147. 1924.

APRICOT

235. Pl. Dis. Rep. Sup. 33:37, 113. 1924.
236. Pl. Dis. Rep. Sup. 47:259. 1926.

BARBERRY

237. Pl. Dis. Bul. Sup. 5:178. 1919.

BLACKBERRY

238. Pl. Dis. Bul. Sup. 28:373. 1923
239. Pl. Dis. Rep. Sup. 33:130. 1924.
240. Pl. Dis. Rep. Sup. 39:83. 1925.

CHRYSANTHEMUM

241. Pl. Dis. Rep. Sup. 37:390. 1925.
242. Pl. Dis. Rep. Sup. 50:447. 1926.

COTTON

243. Pl. Dis. Rep. Sup. 61:283–284. 1928.

EGGPLANT

244. Pl. Dis. Rep. 9(5):59. 1925.
245. Pl. Dis. Bul. Sup. 3:109. 1919.
246. Pl. Dis. Bul. Sup. 10:260. 1920.
247. Pl. Dis. Bul. Sup. 16:278. 1921.
248. Pl. Dis. Bul. Sup. 22:407. 1922.
249. Pl. Dis. Bul. Sup. 26:150. 1923.
250. Pl. Dis. Rep. Sup. 34:237. 1924.
251. Pl. Dis. Rep. Sup. 41:307. 1925.
252. Pl. Dis. Rep. Sup. 45:144. 1926.
253. Pl. Dis. Rep. Sup. 54:327. 1927.
254. Pl. Dis. Rep. Sup. 59:88. 1928.
255. Pl. Dis. Rep. Sup. 61:296. 1928.

[42] A mimeographed pamphlet issued by the Bureau of Plant Industry, U. S. Dept. Agr. Early issues of this publication appeared under the name *Plant Disease Bulletin*.

LOGANBERRY

256. Pl. Dis. Rep. Sup. **52**:90. 1927.

MAPLE

257. Pl. Dis. Rep. **10**(11):137. 1926.
258. Pl. Dis. Bul. Sup. **17**:297. 1921.
259. Pl. Dis. Bul. Sup. **23**:459. 1922.
260. Pl. Dis. Bul. Sup. **29**:421–423. 1923.
261. Pl. Dis. Rep. Sup. **37**:373. 1925.
262. Pl. Dis. Rep. Sup. **42**:333. 1925.
263. Pl. Dis. Rep. Sup. **50**:431, 432. 1926.
264. Pl. Dis. Rep. Sup. **55**:347. 1927.
265. Pl. Dis. Rep. Sup. **61**:284. 1928.
266. Pl. Dis. Rep. Sup. **65**:405–406. 1928.

MENTHA SP.

267. Pl. Dis. Rep. Sup. **50**:474. 1926.

MICHAELMAS DAISY

268. Pl. Dis. Rep. Sup. **50**:457. 1926.

OKRA

269. Pl. Dis. Bul. Sup. **3**:113. 1919.
270. Pl. Dis. Bul. Sup. **10**:265. 1920.
271. Pl. Dis. Bul. Sup. **16**:283. 1921.
272. Pl. Dis. Bul. Sup. **26**:155. 1923.
273. Pl. Dis. Rep. Sup. **34**:239. 1924.
274. Pl. Dis. Rep. Sup. **41**:308. 1925.
275. Pl. Dis. Rep. Sup. **54**:339. 1927.
276. Pl. Dis. Rep. Sup. **61**:297. 1928.

PEACH

277. Pl. Dis. Bul. Sup. **20**:83–84. 1922.
278. Pl. Dis. Bul. Sup. **28**:344. 1923.

PEONY

279. Pl. Dis. Rep. Sup. **37**:402. 1925.
280. Pl. Dis. Rep. Sup. **50**:461. 1926.

POTATO

281. Pl. Dis. Bul. **1**(1):15. 1917.
282. Pl. Dis. Bul. **1**(2):32. 1917.
283. Pl. Dis. Bul. **2**(9):158. 1918.
284. Pl. Dis. Bul. **2**(10):187. 1918.
285. Pl. Dis. Bul. **4**(5):75. 1920.
286. Pl. Dis. Bul. **4**(8):117. 1920.

287. Pl. Dis. Bul. **6**(6):112. 1922.
288. Pl. Dis. Rep. **7**(7):85. 1923.
289. Pl. Dis. Bul. Sup. **2**:47. 1919.
290. Pl. Dis. Bul. Sup. **10**:190. 1920.
291. Pl. Dis. Bul. Sup. **16**:196. 1921.
292. Pl. Dis. Bul. Sup. **26**:47. 1923.
293. Pl. Dis. Rep. Sup. **34**:149, 169. 1924.
294. Pl. Dis. Rep. Sup. **45**:27. 1926.
295. Pl. Dis. Rep. Sup. **54**:233–234. 1927.
296. Pl. Dis. Rep. Sup. **59**:94, 104. 1928.
297. Pl. Dis. Rep. Sup. **61**:238. 1928.

RASPBERRY

298. Pl. Dis. Rep. **6**(9):144. 1922.
299. Pl. Dis. Rep. **8**(7):84. 1924.
300. Pl. Dis. Rep. **9**(5):58. 1925.
301. Pl. Dis. Bul. Sup. **1**:35. 1919.
302. Pl. Dis. Bul. Sup. **20**:112. 1922.
303. Pl. Dis. Bul. Sup. **28**:344. 1923.
304. Pl. Dis. Rep. Sup. **33**:127. 1924.
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EXPLANATION OF PLATES

PLATE 1*

Taf. IX, Fig. 1 bis 11. *Verticillium albo-atrum.* Fig. 12 bis 15. *Periola spec.*

Fig. 1. V. atro-album, Bildung des Dauermycels in den Zellen des faulenden Stengels Form A (380/1).

Fig. 2 u. 3. Keimende Dauerzellen (660/1).

Fig. 4. Reife Conidien von V. atro-album von Form B und C (940/1).

Fig. 5. Ebensolche von Form A (940/1).

Fig. 6 und 7. Keimende Conidien von Form C (940/1).

Fig. 8. Entstehung eines Zwergconidienträgers direkt aus der Conidie (940/1).

Fig. 9. Keimende Conidien. Form A. (940/1).

Fig. 10. Aeltere Keimungsstadien. Form A. (660/1).

Fig. 11. Bildung von Conidien auf kurzen Seitenzweiglein an einem älteren Mycelfaden aus einem braunen Fleck des unterirdischen Stengeltheils. Form C. (940/1).

Fig. 12. a reife Conidie von Periola, b drei andere in den ersten Keimungsstadien (940/1).

Fig. 13. Aeltere Keimungsstadien in Wasser, Bildung brauner Körper an den Keimschläuchen. (660/1).

Fig. 14. Junges Stroma von der Seite gesehen. (540/1).

Fig. 15. Junges Stroma, welches die Epidermis durchbrochen hat (540/1).

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* The legend accompanying plate 1 is a verbatim copy of the legend accompanying plate IX in Reinke and Berthold's paper (149). The typographical errors occur in the original.

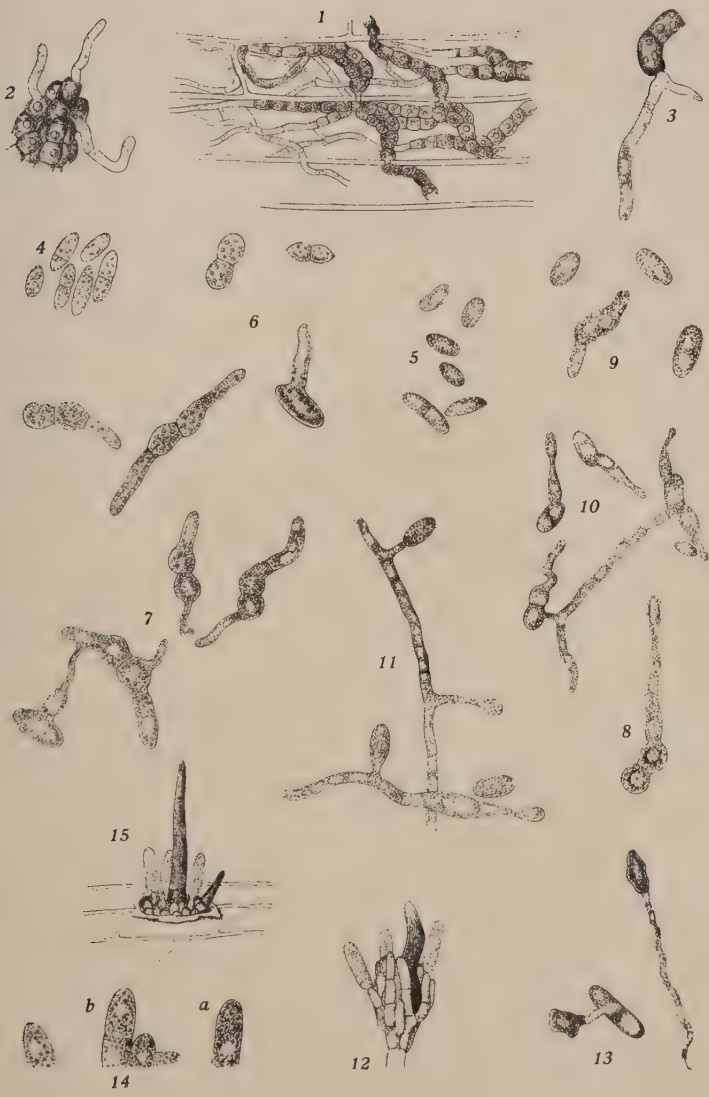
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PLATE 2*

Taf. VIII. *Verticillium albo-atrum.*

Fig. 1. Unterirdischer Stengeltheil einer kranken Kartoffelpflanze, Form C; die bräunlichen Flecke der Rinde sind dicht von Mycelium erfüllt (natürliche Grösse).

Fig. 2. Parenchymzelle der Rinde mit dem Mycel von Verticillium albo-atrum und den sehr feinen Mycelfäden, welche nicht selten accessorisch auftreten. Form C (380/1).

Fig. 3. Mycel von V. albo-atrum in den Stengelgefässen; bei a Abschnürung einer Conidie. Form A (380/1).

Fig. 4. Conidienträger von V. albo-atrum. Form C (380/1).

Fig. 5. Theil einer Bastzelle mit Mycel von V. atro-album, die Wandung an einzelnen Stellen durchbohrt. Form A (660/1).

Fig. 6. Junger Conidienträger. Form A (380/1).

Fig. 7. Conidienträger mittlerer Grösse aus einem Haar des Kartoffelstengels hervortretend. Form A (380/1).

Fig. 8. Aeltere Conidienträger, deren untere Zellen braun geworden sind und zum Theil neue Septa gebildet haben. Form A (280/1).

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* The legend accompanying plate 2 is a verbatim copy of the legend accompanying plate VIII in Reinke and Berthold's paper (149). The typographical errors occur in the original.

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PLATE 3.

Photographic reproduction of sclerotia-like bodies drawn by Ernst Hallier (Plate III, figs. 1 and 2).

Hallier simply described his drawings as: "Fig. 1. Conidienhaufen im Stengelgewebe der Kartoffel, gezeichnet mit System D." "Fig. 3. Conidia septata; System F." (Photograph, natural size.)

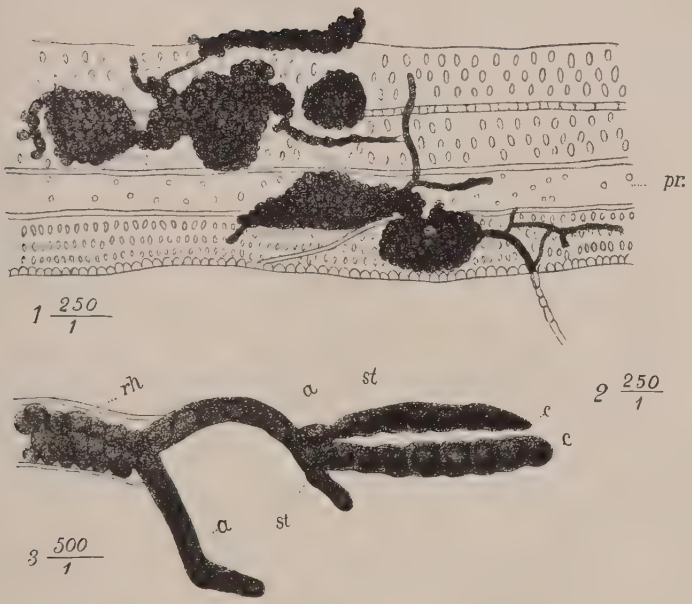
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PLATE 4

Photographic reproductions of van der Meer's figures of *Verticillium albo-atrum* (fig. 1) and *Verticillium dahliae* (figs. 2 and 3). Photograph, slightly reduced. The following is a verbatim copy of van der Meer's legends:

Fig. 1. *Verticillium albo-atrum* (potato) on cherry agar, 10 days old: filamentous black resting mycelium. × 7.

Fig. 2. *Verticillium Dahliae* (dahlia) on cherry agar, 10 days old: microsclerotia. × 9.

Fig. 3. *Verticillium Dahliae* (potato) on cherry agar, 10 days old: microsclerotia. × 9.

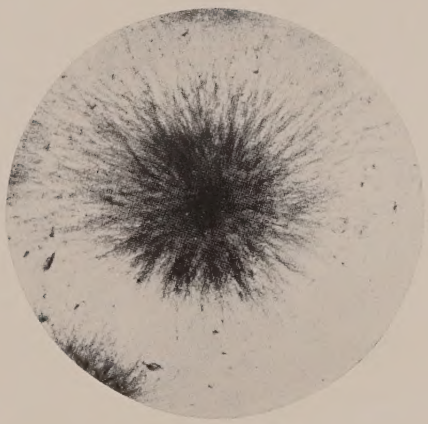

Fig. 1. *Verticillium albo-atrum* (potato) on cherry agar, 10 days old: filamentous black resting mycelium. × 7.

Fig. 2. *Verticillium Dahliae* (dahlia) on cherry agar, 10 days old: microsclerotia. × 9.

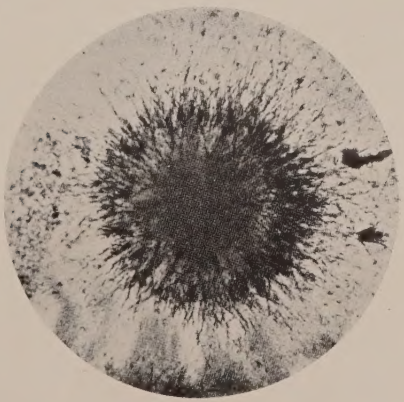

Fig. 3. *Verticillium Dahliae* (potato) on cherry agar, 10 days old: microsclerotia. × 9.

The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.

5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.

6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.

7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.

8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. R. Hoagland and J. C. Martin. July, 1923.

9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.

10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.

11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.

12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.

14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.

16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.

17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.

18. Factors Influencing the Rate of Germination of Seed of Asparagus Officinalis, by H. A. Borthwick. March, 1925.

19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.

20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.